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Speciation, Species Concepts, and Biogeography Illustrated by a Buckwheat Complex (Eriogonum corymbosum)

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SPECIATION, SPECIES CONCEPTS, AND BIOGEOGRAPHY

ILLUSTRATED BY A BUCKWHEAT COMPLEX (*ERIOGONUM CORYMBOSUM*)

by

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ABSTRACT

Speciation, Species Concepts, and Biogeography Illustrated by

a Buckwheat Complex (*Eriogonum corymbosum*)

by

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Utah State University, 2009

Major Professor: Dr. Paul G. Wolf
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The focus of this research project is the complex of infraspecific taxa that make up the crisp-leaf buckwheat species *Eriogonum corymbosum* (Polygonaceae), which is distributed widely across southwestern North America. This complex provides an ideal taxonomic group for research into population relationships and speciation. To avoid unnecessary debates about taxonomic validity or contentious issues regarding appropriate species definitions, the historical evolution of the species concept is first reviewed in detail, demythologizing an often-assumed species problem. Following that review, the *E. corymbosum* complex is examined specifically.

Although eight varieties of *E. corymbosum* are currently recognized based on morphological characters, this group of large, woody shrubs has a history of revisions that demonstrates the uncertainty inherent in circumscriptions based on morphology

alone. The apparent rarity of some *E. corymbosum* varieties also presents conservation and management challenges, demonstrating the need for taxonomic verification.

To bring greater resolution to this group, I genetically tested samples from populations of six of the eight varieties of *E. corymbosum*, as well as a number of related buckwheat species. With 103 AFLP loci and chloroplast sequence data from 397 samples, I found strong support for the designation of the recently named *E. corymbosum* var. *nilesii*. This predominantly yellow-flowered variety had previously been considered part of a more common variety, and thus its management had not been of particular concern. But as a separate variety, its known distribution is quite limited, and management for this rare plant is now advised.

An examination of the biogeography of the *E. corymbosum* complex provides further support for the apparent rarity of var. *nilesii*, as well as var. *aureum*. Both taxa are found at the periphery of the complex, and both may represent insipient species. While all other varieties appear more closely related to each other than to varieties *aureum* and *nilesii*, with overlapping ranges confined mostly to the Colorado Plateau, both var. *aureum* and var. *nilesii* appear to have allopatric ranges largely off the Colorado Plateau. It appears these two peripheral varieties may each entail a separate center of origin for two new taxa.

(185 pages)

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CHAPTER 1

INTRODUCTION

One hundred and fifty years after Charles Darwin (1859) provided the mechanism and evidence that finally convinced the scientific community that species actually do evolve, evolutionary biology has become the cornerstone of all areas of biological research. Although Darwin was working without the benefit of computers or electron microscopes, and without the knowledge of genetics or plate tectonics, many of his theoretical ideas have stood the test of time (Mayr 2000; Bowler 2009; McClure 2009). Rather than resulting in a new and better theory of species evolution, a deluge of new research that his theory unleashed has largely substantiated and enriched his theory. However, the twisting path to our current understanding of species has been strewn with controversy as the finer details of biodiversity have been, and continue to be, uncovered (Baum 2004; de Queiroz 2005b).

The following three chapters examine speciation – the process, how to recognize it, and its place in the taxonomic hierarchy – as well as the evolution of our understanding of species. In my view, speciation is a messy process, and not all individuals can be assigned to a species. Unlike more inclusive taxa, such as genera, families, and higher ranks (which are categorical constructs used to help organize the biological world), species are real entities, units of evolution, and key components of biodiversity (Wiley and Mayden 2000; Ghiselin 2002; de Queiroz 2005b; Rieseberg et al. 2006). Although the historical controversy surrounding the nature of species and the

validity of species concepts (Stamos 2003; Baum 2004; Reif 2005) is long and seems intractable, I will argue that resolution is possible.

In Chapter 2, I begin with views of species held by the ancient Greeks, and follow the evolution of the concept through the Roman Empire and the Middle Ages, to its transformation by Darwin and Wallace, and the difficult road it has traveled since. During this long and often sordid history, the so-called species problem became entrenched, developing an inertia that has not flagged, even though most of the challenges that propelled it have been answered. In Chapter 2, I attempt to lay this problem to rest by arguing that the concept has been successfully defined and understood for decades, and that most of the debates are tempests in a teapot.

Infraspecific taxa often make up the body of an established species, and they are capable of budding off as incipient species themselves. While a species can sometimes be difficult to identify, recognizing infraspecific taxa is messier still (Wake 2006; Mulcahy 2008). After addressing the validity of the species concept and the nature of species as units of evolution in Chapter 2, I consider the process itself in Chapter 3 with an examination of a widely distributed species composed of populations that belong to multiple biotypes considered to be varieties. By comparing individual samples of this species genetically, I address the validity of one of those varieties. The individuals sampled from those populations did in fact demonstrate recognizable genetic cohesion along with separation as a group from the other varieties, leading me to conclude that its varietal status is warranted. Had I found that the samples from these populations were not separable from another variety based on the genetic evidence, I would have

recommended that they be subsumed within the variety with which they were most closely associated.

In Chapter 4, I look at this same species complex biogeographically as an entity in the process of speciation. I examine the arrangement of and variation within its parts, and from that information attempt to uncover clues to its past as well as its future. To do this, I dredge up and dust off an old model of historical biogeography that once had its day but is currently out of fashion. Science can be a slash-and-burn process, as I discovered when I investigated the species problem. Once a new tool or principle is created or discovered, it can be wielded like a scythe, mowing down past practices and concepts. But this practice can lead to valid ideas being cut down in the process. Such was the case for the center-of-origin concept, employed by Darwin (1859), Adams (1902), Matthew (1915), Brown (1957) and others until the later half of the 20th century when new discoveries led researchers to lay it low (MacDonald 2003; de Queiroz 2005a). One discovery made during the early 20th century – that continents move (Wegener 1929; Hamblin 1975) – was so dramatic, awe-inspiring, and revolutionary, that researchers saw vicariance in their dreams, and the center-of-origin concept with its dispersalist underpinnings, suddenly lost its appeal. In this chapter, I dig it back up, brush it off, and try it out on the *Eriogonum corymbosum* complex of varieties, arguing that at shallow taxonomic levels, the center-of-origin model provides a potentially useful approach to examine a group's historical biogeographical development.

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CHAPTER 2

THE MYTH OF THE SPECIES PROBLEM

INTRODUCTION

Debates about species, like honest debates about biological evolution between researchers in the field, are both useful and important, particularly as technologies for detecting species expand and improve, and our understanding of speciation is refined. Most of today's debates center on the best way to define the species category (i.e. the taxonomic rank in the Linnaean system). Over 20 species concepts have been proffered for consideration, and more will likely be developed. These competing concepts promote the impression of a conflagration of incompatible ideas. But a clear understanding of species – covering an overarching concept that defines the species category, the taxonomic category itself, and individual species taxa – was clarified over 30 years ago. The oft mentioned "species problem" is usually referred to tangentially because it has no clear definition. It is, instead, historically multifaceted, with many incarnations, nearly all of which have been addressed and settled. But during its long life it somehow gained an inertia it does not merit. It achieved a status of familiarity, of permanence, something to accept as a given. But the species problem is a myth.

A species taxon is composed of organisms in one or more populations that form a cohesive, reproductive unit – a separate lineage on its own evolutionary trajectory (Zimmerman 1959; Simpson 1961; Hennig 1966; Wiley and Mayden 2000; Ghiselin 2002; de Queiroz 2005; Rieseberg et al. 2006). This overarching concept has been clearly described, yet a debate continues by proponents of other species concepts as if it

had not. Critical to this overarching concept is the recognition that species taxa are individual entities, rather than classes of organisms (Ghiselin 1974; Hull 1976; Mayden 1999; Wiley and Mayden 2000), and the most incorporative units upon which evolution works (Ghiselin 2002). Although these concepts are simple, understanding them does not eliminate problems. How separate and cohesive must a population or group of populations be to achieve species status? How is separation measured or determined? When do we know speciation has occurred? When is speciation potentially occurring but not yet complete? What are the merits of insipient species? These are problematic challenges, but they do not threaten the legitimacy of the overarching concept that gives biological evolution its foundation. To the contrary, the process of speciation demands that such questions be addressed, and the questions themselves bolster the validity of the overall species concept.

The mythical aspect of the species problem is much broader and more deeply rooted than the current debate regarding which species concept most accurately defines the species category. This indelible myth is enhanced and propelled by an amorphous amalgam of mostly faulty ideas long-since debated and discarded yet repeatedly repackaged and recycled. Like a horror movie of undead miscreants whose corpses keep getting back up, incorrect ideas and settled arguments continue to bedevil us. These include errant notions about species taxa, such as the view that they are unchanging entities, or that they are classes with definable class members, or that they are merely useful but otherwise unreal human abstractions. The degree of confusion is enriched when the term "species" is used without clarifying whether one is referring to a specific taxon or to the category itself. As a result, there seems to be a nearly universal

presumption that a clear, broadly accepted understanding of the species category is unattainable.

The way in which the subject of species is presented in introductory texts tends to validate the perceived problems rather than resolve them. Many high school and college textbooks include discussions of the term "species" without clarification, and introduce species concepts a la carte. In so doing, they confuse rather than edify, further entrenching rather than dismantling the myth (e.g. Strickberger 2000; Futuyma 2005; Freeman and Herron 2007). This is unfortunate, since repudiation of the species problem can be effectively achieved through educational curricula that fully address the ontological foundation of species concepts.

The species problem from past to present

The species problem has a long history. Its foundation dates back to incorrect ideas regarding the nature of reality as conceived by ancient Greek philosophers. Plato, and other influential thinkers, viewed each species as a unique, immutable, and eternal entity. The real organisms we see in nature were, to these philosophers, flawed replications of eternal, perfect forms (Hull 1965a; Loomis 1969; Mayr 1982). From ancient times until well into the 19th century, versions of Plato's static conception of species taxa based on mystical ideal forms were presumed to be true. In this respect, for over two millennia the species concept was, although incorrect, relatively problem free. The myth of today is rooted in the sheer duration of this errant idea of stasis.

Darwin's contributions in the 19th century finally provided a basis for a realistic understanding of species taxa. But his discovery (Darwin 1859) of a functional

evolutionary mechanism – natural selection – presented a view diametrically opposed to the age-old belief in species as immutable taxa. Even though the new explanation fit the evidence of locally adapted species and fossil evidence suggesting species variation over time as the old view could not, it was ontologically too revolutionary and theologically too subversive. As a result, in spite of Darwin's clear explanation and supportive evidence, the species problem was born at this distressing nexus of scientific discovery and historical dogma.

Mendel's contributions, which came to light in the early 20th century (providing the evidence for the heritable variation that Darwin's theory required for species change), again paradoxically generated more contention than coherence. Uncertainty prevailed with continuing debates within the scientific community between the so-called Darwinians (biometricians) and Mendelians regarding the process of evolution and the nature of species (Provine 1982; Nordmann 1992). Although the two contentious schools of thought eventually merged harmoniously by the 1940s into the Modern Synthesis, the alliance failed to end the debates surrounding species (de Queiroz and Donoghue 1988; Stamos 2003).

The discovery of DNA structure by Watson and Crick in 1953, and the cracking of the genetic code shortly thereafter, would lead to development of phylogenetic systematics (Hennig 1966), providing the puzzle pieces necessary to assemble an accurate understanding of species taxa and the species concept as described in the introduction of this chapter. But by then, the uncertainty surrounding species concepts was so thoroughly established that a broad consensus on the issue remained elusive, and the species problem had gained the status of myth.

The exceedingly long history of incorrect ideas regarding species fixity (and the subsequent difficulty in discarding those beliefs), the uncertainty that emerged after the presentation of Darwin's radically different theory, the continuing uncertainty after the convergence of Mendelian and Darwinian viewpoints into the Modern Synthesis, the confusion that persisted even after the genetic code was broken, and the current plethora of competing species concepts have all added to the tangled mess that is today cryptically and cavalierly referred to as the species problem. With so many scientists concurring that the problem exists (e.g. Ridley 1989; O'Hara 1994; Mishler 1999; Cracraft 2000; Mayr 2000; Stamos 2003; de Queiroz 2005; Ereshefsky 2007), it has taken on a life of its own. In my view, the often-referenced species problem rarely has a clear description, but signifies instead a widely held assumption that arriving at consensus for the species concept is problematic if not impossible. The myth is that a problem exists, when in fact few can articulate what the problem is, and those who can describe it differently, or they begin to tick off the many challenges the concept has faced (rectify one and they will provide another, then another). An unfortunate aggregation of conflicting ideas and recycled debates has prevailed due to a failure of education, which could otherwise bring an end to this durable but unnecessary myth.

What is everyone talking about?

Confusion begins with the unadorned term "species." This word is ambiguous when used without clarification since it can refer to a number of distinctly different but related ideas, including (1) a particular species taxon, (2) the taxonomic category of species, or (3) a concept defining the members of the species category. Each of these

unambiguous ideas has been accurately explained by others (Hull 1965a, 1965b, 1976; Ghiselin 1966, 1974; Mayden 1999; Wiley and Mayden 2000) so I am not offering anything new in that regard. However, using these terms unambiguously will help bring clarity to this subject.

An appropriate understanding of species concepts will help guide research and accelerate the detection of, and solutions to, pressing problems of biodiversity conservation, unrecognized and preventable extinctions, and ecosystem decline. Thus the goals of this chapter will be to explain the species problem – its historical evolution and unfortunate and unnecessary persistence – and explain how to dismantle it by deconstructing the canards that support the problem and restating the ontological reality of species taxa and the overarching species concept.

The multiple meanings of "species"

Lack of specificity regarding the three possible meanings mentioned above for the term "species" contributes to the species problem. Species as taxa in nature are individuals (Ghiselin 1974, 2002; Hull 1976) and as such, each is a real entity (discussed in detail under ***Classes versus Individuals*** below). A common error that reinforces the mythical species problem is that each species taxon is not an individual but a class whose members are individuals (i.e. organisms) within one or more populations. If each species taxon is a class, then each of them can be defined. As a result, many attempts have been made to define individual species in nature (Ghiselin 1984; Stamos 2003). But individuals tend to defy definition since no individual is exactly the same from one moment to the next. When a taxon is viewed as a class, the inability to define its

membership – with a reliable character set that is both necessary and sufficient – bolsters the mythical species problem since the taxon's reality becomes suspect. Recognizing species taxa as individuals eliminates this difficulty, since individuals are, by definition, indefinable but identifiable.

The species category (or rank) is a level in the organizational system codified by Linnaeus – one of many hierarchical taxonomic groupings, each definable. The species category is a class whose members are all extant species taxa (Hull 1976). Yet, like the other taxonomic categories in this organizational system, it is an artificial construct. Carelessness with this term bolsters the myth. Because the species category is an artificial entity, its individual members – the species taxa – can mistakenly be viewed as artificial as well (Burma 1949; Mishler 1999). In this way the myth is supported by an artifact of rhetorical confusion.

The species concept broadly defines the species category, providing the ontological essence of any and all species taxa. It has a long history with many incarnations (often coexisting as competing concepts), the most extreme being the variation between its pre- and post-Darwinian expressions. Currently there are more than a score of competing species concepts (Mayden 1999; Avise 2000; Stamos 2003; de Queiroz 2005). Although some may be less than rational, most are logically justifiable and functional concepts, each providing an operational definition for the discernment of a species (Ghiselin 2002). Yet the multiplicity of these concepts contributes to the mythical species problem because they are considered to be in competition (Ghiselin 2002; de Queiroz 2005). But given that each functional operational method is a means of discovery rather than an exclusive definition, those concepts provide additional methods

for recognizing species in nature. The myth is bolstered by the presumption that each is incompatible with the others and only one can be the most accurate.

A western perspective

I am approaching the species concept from a historically western perspective and have not examined the history of species concepts among other cultures. It may well be that other cultures had very different and possibly more accurate views of species compared to those developed in Europe and the Ionian middle east beginning in the 7th century before the Common Era (BCE). But in my view, the confusion about species that exists today – which emerged after the development of the Modern Synthesis – had its origins in western philosophy, religion, and science. Therefore, I am compelled to examine species concepts from this historical perspective in order to dissect and dismantle the current mythology.

Plato's mystical edict suggested that, even with the variation inherent to the vagaries of life, species would, over the generations and even the eons, remain static and unchanging, forever governed by their ideal forms. It was not until religious clerics began doing real science in the name of God at the close of the Middle Ages that fuzzy notions of an ongoing process of speciation finally received serious attention (Richards 1992). The science of those theologians led inexorably to Darwinian Theory, and to the debate about the true nature of species that continues today.

Myths are remarkably resilient. They gain a presence that, like the phantom pain of an amputee's missing limb, can exist in spite one's rational awareness. Once established, the tenets and corollaries of myths become reflexive beliefs, even when the

myth itself is expressly denied (Mayden 2002). Artifacts of Plato's fantasy of ideal forms still bedevil us in the guise of type specimens, species taxa as classes, and definitions for species taxa. The endless debates themselves lend undue credence to the species problem. Awareness of the history of species concepts will help deconstruct this myth, elucidate the intellectual traps, and reduce the reflexive acceptance of this largely unsupportable notion.

The Early Development of Species Concepts

In the writings of ancient Greeks are found many of the valuable ideas that gave rise to modern science. But along with them came errant speculations, some of which promoted supernatural beliefs. Ionian philosophers, particularly those from the Milesian school, gave us hints of evolutionary theory, species change, and a universe run by natural laws, yet they also theorized the earth was floating on water and that all matter was born of water. Pythagoras and his students developed useful geometric formulas while also promoting reincarnation, the mystical music of the spheres, and numerology governing all things we perceive. Although the ideas of Socrates, Plato, and Aristotle helped codify rationality and catalyze science, they also promoted imaginary perfection, eugenics, class separation, and despotism.

From these pioneering philosophers and scientists came two competing theories – species stasis versus species change – and eventually stasis won out. The ancient origin of the idea of species stasis, combined with its connection to the giants of intellectual thought followed by theological incorporation and centuries of perceived certitude, elevated this concept to the rarefied air of myth. Yet this mythical status with its mystical

misapplications was to a large extent an accident of history followed by political and theological persuasion rather than a natural outcome of pre-scientific cultures. The ideas of the ancient theorists that had traction were, as is often the case today, those that gained political support. Their establishment was more a matter of public relations and education than perceived scientific validity. There was no system of scientific peer review or a scientific method with which to examine and test Plato's proposals. His fallacious ideal forms for each species were adopted and modified in the early centuries of the Common Era by those with a stake in mysticism who were skilled at propaganda (and Creationists continue the practice today). Although the views of species permanence and definability proffered by Plato and others were far from the mark, the opportunity and the building blocks for a more accurate direction of thought were there all along. Unfortunately those better ideas had neither the advantages of history nor the benefits of political promotion.

The Ionians

Many historians point to the city of Miletus and the school founded there by Thales as the birthplace of western philosophy and science (Durant 1953; Fuller and McMurrin 1957; Green 1973). This port city of immigrants on the eastern coast of the Aegean Sea was an important trading center – for both goods and ideas. Revolutionary ideas flourished in this metropolitan nexus between Africa, Europe, and Asia without a severe threat of persecution (Mayer 1950). In the School of Miletus, Thales and his students worked as scientific philosophers seeking answers to the nature of the universe without recourse to supernatural explanations (Fuller and McMurrin 1957). They knew

then, perhaps as well as we know now, that miraculous accounts are merely admissions of ignorance.

Thales (640-550BCE) founded his school on proceeds from a successful career trading in olive oil. He was a philosopher, astronomer, and mathematician who argued the sun and stars were not gods at all, but balls of fire and that the earth floated on water (Durant 1953; Fuller and McMurrin 1957). He also argued that the fundamental element of all matter was water (Serafini 1993). Perhaps his most important contribution was the abandonment of supernatural explanations for earthquakes, volcanic eruptions, solar eclipses, the stars, and other cosmic mysteries (Mayer 1950). Following his lead, the Milesians and other Ionian philosophers sought natural solutions and natural laws (Serafini 1993).

Thales' student Anaximander (610-546BCE) appears to have taken a leap forward by describing the universe as limitless, challenging the more common viewpoint of earth enclosed by a heavenly and decidedly finite vault (Mayer 1950; Fuller and McMurrin 1957). Anaximander's cosmos was composed of infinite worlds coming into being and going extinct. He is even said to have argued that the earth floated free in space (rather than on water), as do the other celestial bodies, some of which are further away than others. Here on earth, Anaximander argued life originally formed in the sea, but was driven on land as the waters receded, and forced to develop the ability to breath air. He even argued humans evolved from simpler fish-like marine forms, believing humans could not have originally survived in our present form with such a long period of helplessness before adulthood (Mayer 1950; Popkin et al. 1999). His prescient hints at

cosmological and biological evolution demonstrate a direction science might have taken. Instead, it would take well over 2000 years for scientists to return to these views.

Other Milesians also produced dramatically prescient hypotheses. Anaximenes (570-500BCE) argued that the single elemental component fundamental to all matter was not water but air, and that all forms of matter (from fire to solids) were aspects of a continuum of air's variation (Popkin et al. 1999). Challenging Anaximenes' theory, Anaxagoras (500-428BCE, from another Ionian city north of Miletus) viewed the elements as unlimited, with each unique solid made of its own stuff (Fuller and McMurrin 1957; Crombie 1967). Anaxagoras fortified the idea of diversity's continuum with the suggestion that nothing perishes or comes into being (Popkin et al. 1999). Instead, all things form from preexisting matter brought together, and all things only appear to perish when their constituent parts separate (Graham 1994). Furthermore, he extended his theories of matter to the cosmos, presuming the moon was made of earth with a surface of plains and ravines, the sun was not a god but a red hot stone mass, and the stars were like the sun but merely father away (Fuller and McMurrin 1957; Popkin et al. 1999). These creative viewpoints led to a death sentence for impiety in his adopted city of Athens, which he avoided by returning to Asia Minor (Mayer 1950). Regarding biology, he said animals originated from moist environments, and then afterwards from other animals, and he gave no special origins for humans (Mayer 1950). In fact, he hypothesized that human intelligence was an outcome of forelimbs freed from the task of locomotion, hinting at evolutionary change, and even selective opportunity (Popkin et al. 1999).

These students of secular (rather than celestial) cosmology were seeking natural laws to explain their world and even the universe. Given that this was a time before systematized experimental methods and before the invention of many technological tools such as microscopes and telescopes, their ideas regarding matter, diversity, and species change demonstrate a propitious path that might have been taken. Although their attempts at rational solutions to natural mysteries often included details that were misguided or completely erroneous, their conjectures occasionally pointed to concepts of species and evolutionary change that were surprisingly perceptive. Had their visions of reality continued to be pursued without the threat of theological and political interference, their emerging rational ideas would have inevitably (with the assistance of technological and scientific methods) opened the door for someone like Darwin to pass through in a considerably earlier time. Instead, fanciful concepts of species stasis gained authority, contributing to an intellectual and conceptual u-turn. That misdirection was later hardened by the influence of religious fundamentalists who, without compunction, co-opted science for their own purposes, helping steer western civilization down a path to the Dark Ages.

The Pythagoreans

The Miletus school came to an end after the city of Miletus was conquered by Persians in 494BCE, and due to the brutal repression there, many Ionian philosophers fled west to Sicily and Italy (Mayer 1950). Pythagoras (582-507BCE) was born in the nearby town of Samos and was influenced by Thales, Anaximander, and Anaximenes (Fuller and McMurrin 1957; Grant 1989). He emigrated to Croton in southern Italy

where he founded a coed cult of vegetarian mathematicians who led ascetic lives to prepare for their reincarnation into the next life (Morrison 1956). He and his acolytes, unlike the Milesians, linked decidedly more mystical components to their theoretical explanations for reality (Fuller and McMurrin 1957; Grant 1989). Although many of Pythagoras's ideas appear to be those of a crank, a series of chance events would eventually result in their widespread establishment, versions of which would eventually come to dominate western thought for over two millennia. These accidental events, assisted by political maneuvers, would relegate what had been the nascent emergence of more rational scientific thought from Ionian philosophers to a slumber from which secular biological science would not be fully re-awakened until the discoveries of Darwin and Mendel.

Pythagoras and members of his order made important advances in mathematics, particularly regarding the proportions relating to harmonic intervals in music (Jones 1969). The impact of mathematics – with its alluring intimation that there were laws of nature that could be defined and quantified – was addictive, as were mystical explanations for cosmic phenomena, and the Pythagoreans combined the two. It was they who established the idea of a cosmic symphony of musical notes created by the movements of heavenly bodies, which would come to be known as the harmonious "music of the spheres" (Fuller and McMurrin 1957). They saw numbers as the reality behind all things – from corporeal objects to abstractions. These not only included geometric shapes, but more subjective concepts such as morality and justice, and speculative ideas such as the origin of the universe (Jones 1969; Dudley 1997).

The ideas of the Pythagoreans were an entertaining mix of rationality and pseudoscience. Although Pythagoras and his followers have been associated with mathematical formulas such as the Pythagorean Theorem, they are less well known for their mysticism – such as claims of out-of-body travel and the establishment of the pseudoscience of numerology (Serafini 1993; Dudley 1997). Their ideas and activities would eventually reach Plato (or more accurately, he would reach them) in a remarkably roundabout way, and he would modify the Pythagorean view of numbers behind all things in a fashion that would infuse species with the notion of stasis while maintaining the element of mysticism.

Competing with Pythagoras for the developing views of the cosmos was Heraclitus of Ephesus (540-480BCE). Heraclitus proposed that things are in a constant state of change – that nothing remains the same except change itself (Jones 1969; Robinson 1987). In his view, "everything flows, nothing stands still." Heraclitus felt that all things are but one thing, and that opposites contribute to this unity: "The harmonious structure of the world depends upon opposite tension like that of the bow and the lyre... Opposition brings concord. Out of discord comes the fairest harmony" (Robinson 1987). In light of these statements, perhaps he grasped the ideas of competition, ecological balance, and evolutionary change, as well as the value of biological diversity. He provided a dramatic and poetic analog to the phrase "survival of the fittest" with his statement that "Through strife, all things arise and pass away... War is the father and king of all: some he has made gods, and some men, some slaves, and some free." And in support of that concept he noted that, although nothing lasts forever in one form, the

natural law that governs change is constant, "This order, the same for all things, no one of gods or men has made; but it always was, and is, and shall be."

Unfortunately, Heraclitus was the last clear proponent of change in nature until the 18th and 19th century biologists Lamarck, Wallace, and Darwin began to propose compelling theories about species origins (Mayer 1950). Heraclitus dramatically stated his view of the random chance inherent in the universe with his statement that "Time is a child playing dice" (Robinson 1987). The ideas of Heraclitus were so far afield from what would become Plato's worldview that they may have, ironically, contributed to Plato's extreme concept of ideal forms. For Plato was threatened by change. In his view, a changing world would be unknowable (Irwin 1977). Thus, more than a century after Heraclitus penned his ideas, Plato clung to his ideal forms because they provided him with what he considered a knowable reality from which the material world emerges.

The undoing of the Pythagoreans was not their peculiar doctrines, but their alliance with aristocratic forces (Mayer 1950; Fuller and McMurrin 1957). The political winds in the west eventually turned against them, and many were killed and most of their schools were abandoned (Grant 1989). Although much of what we think we know about Pythagoras may be apocryphal, including his discovery of the theorem that bears his name (Drake 1970; Veljan 2000), his influence, and subsequently that of his followers, was real (Serafini 1993). After the network of Pythagorean communes lay in ruin, Pythagorean essentialism would be resurrected and preserved by Plato, ironically in response to those same winds of political unrest (Mayer 1950).

The Socratics

Socrates (469-399BCE) was considered by many of his contemporaries as the wisest and happiest of men (Mayer 1950; Popkin et al. 1999). This Athenian son of a sculptor and a midwife served with honor as a soldier (Mayer 1950; Fuller and McMurrin 1957; Jones 1969) and associated with the upper class of Athens. Eventually he found his calling as a teacher. He spent the rest of his life neglecting his wife and two sons, supported by his aristocratic circle of friends while tending to the students who adored him and to any other willing conversationalists (Durant 1953; Wood 1974). His development of philosophy would deeply affect the views of his two most gifted intellectual descendents, Plato and Aristotle, and through them determine the direction of science and a mythical foundation for species for the next two millennia.

Socrates developed a reverence for the intellect's intuitive power while maintaining an aversion for experiment. Although his views on ethics and morality demanded intellectual rigor, his views on science helped bury the embryonic ideas of evolutionary theory that were being floated by other great thinkers of the time. Rather than examine nature to discover the details of life, Socrates viewed natural science with disinterest if not disdain (Berland 1986).

Socrates played the part of an unthreatening everyman, endlessly questioning his students to help them clarify their thoughts and develop their ideas (Durant 1953; Wood 1974). In so doing, he developed his 'Socratic method' of teaching (Fuller and McMurrin 1957). In his process of feigning ignorance with humorous self-deprecation, Socrates would invite his interlocutors on an intellectual excursion through paradox and carefully-

defined terms to moral insight. In so doing he cajoled others to ignore public opinion and think independently.

Socrates weighed in mainly on ethics and morality rather than science (Mayer 1950; Durant 1953). As he put it, "the people in the city have something to teach me, but the fields and trees won't teach me anything" (Hamilton 1973). Although his intellect was formidable, a naturalist he was not, and fallible he was. His first concern was clarity of thought and meaning (Popper 1983) and his focus was on ideas concerning virtue and justice rather than the nature of the cosmos. His tireless insistence on clear definitions would profoundly affect Plato and Aristotle, both of whom would look beyond humanity and apply his methods to the universe.

Eventually, and perhaps inevitably, his habit of challenging authority, combined with an indefatigable ability to out-duel anyone in debates, eventually drew the wrath of some politicians (Wood 1974). His famous trial (for impiety and corrupting youth), death sentence, and execution were also due in large part to the political conditions in Athens (Wood 1974). Socrates supported the aristocracy, and the democratic movement was in the process of purging that political wing. His own fearless nature and code of ethics prevented him from playing it safe, and he did not make any effort to avoid the death penalty by compromising those ethics. The execution of Socrates was a galvanizing event in the life of Plato, spurring him on to fully develop his own philosophy (Jones 1969; Green 1973).

Plato (428-348BCE), the most successful student of Socrates, was a member of the aristocracy who revered authority and promoted sexism and class division while opposing democracy (Durant 1953; Green 1973). As a known ally of Socrates and

supporter of the aristocracy, Plato's safety was at risk in Athens following the execution of his revered teacher. In the year 399BCE he fled at age 28 to begin a sojourn in exile that would last 12 years (Mayer 1950; Fuller and McMurrin 1957). His experiences would influence his development of philosophy, including a radical perspective on species.

Plato's first stop during his self-imposed exile appears to have been Egypt, where he was impressed by the priestly ruling class of the last Egyptian dynasty (Durant 1953). The efficiently run agricultural state along the Nile had maintained relative social stability for over a thousand years. Who knew that the last Egyptian dynasty would fall to foreign invaders only 50 years later? Plato sailed to Tarentum, Italy, and joined one of the last remaining Pythagorean schools that had survived the purges of aristocratic-leaning organizations (Mayer 1950; Durant 1953). The school consisted of a small group of scholarly men being trained to rule, and he was again impressed. Plato's appreciation for political authority should be seen in light of his desire for transcendent authority and permanence, which are directly related to what would become his views on species stasis and the state of knowledge requiring such permanence.

Plato spent his entire time abroad experiencing and analyzing the cultural wisdom and philosophies of many creeds, while harboring a passion to develop his own, before returning to Athens in 387BCE. Had he not been driven into exile, his close association with an appreciation for Pythagorean ideas may never have occurred, and his contribution to the myth of species stasis might have had considerably less impact, had it occurred at all.

Plato penned his most famous works after his return from exile, and they incorporated ideas from his experiences during that period. While his master's focus had been the ontology of ethics and virtue, Plato was more concerned with political philosophy grounded in a universal theory of everything. Combining the Socratic penchant for definition with the Pythagorean fantasy of formulaic reality, Plato elevated abstract concepts to eternal and intangible templates for all things perceivable, including species.

In his dialogue *Republic* (Durant 1953; Loomis 1969), Plato theorized the ideal organization of society with the necessary political institutions that would reflect his metaphysical view of the cosmos. At the root of Plato's cosmic vision were his mystical ideal forms. He argued that true reality was embodied in these intangible but eternal entities underpinning all the tangible and temporary things we perceive, providing objective templates without which nothing would exist. In Plato's doctrine, these ideal forms should be the objects of scientific examination and knowledge rather than concrete entities sampled from the natural world. Given that ideal forms can be perceived only abstractly, he felt science to be the exclusive domain of philosophers with the training and the refined intuition required for such pursuits (Jones 1969).

Plato was not a fan of change (Keyt 1969), and Pythagoras gave him a conceptual escape from a world that obviously appeared to be in flux. In Plato's metaphysics, physical objects, such as the organisms that make up a species, are merely poor replicas and perishable suggestions of the unchanging, eternal, and perfect forms from which they all spring (Green 1973). The organisms we observe change over time as they develop, age, and deteriorate. Like a square drawn freehand merely resembles the abstraction of a

perfect square, organisms are (according to Plato) but crude reproductions of their ideal species form. If this were true, a species in nature would be a class consisting of set of imperfect corporeal organisms that make up its populations. The eternal ideal form was thus, in Plato's vision, more real than the perishable and temporary material particulars by which it is identified.

Aristotle (384-322BCE) was Plato's most brilliant student. But unlike Plato, and dramatically different than Socrates, Aristotle was a man of science. Son of the Macedonian king's physician, he grew up familiar with scientific tools and techniques. The school Aristotle founded – the Lyceum – was (unlike Plato's Academy of speculative philosophy and mathematics) a center for natural science. After Alexander of Macedonia ascended the throne, he remembered his childhood teacher by commanding hundreds of collectors to supply the Lyceum with all manor of zoological and botanical material from throughout Greece and Asia (Durant 1953), enabling Aristotle to develop the world's first great zoological gardens. With his appreciation for all things tangible, Aristotle broke with his teacher on the concept of ideal forms.

For both Plato and Socrates, definitions and generalities were the pursuits of science. Plato took this to an irrational extreme, giving ideal forms a mystical reality that was separate from, but ruled, the observable world. Aristotle instead saw reality in his living samples – with the forms residing within the particulars – thus demoting Plato's mystical perfection to mere abstract class definitions (Jones 1969). This was an important turn toward rational science and away from mysticism. But Aristotle's appreciation for definition also led to a lasting misunderstanding of species.

Although Aristotle challenged Platonic views on reality, he was (like his teacher and most well-educated Greeks of status) not one to get his hands dirty. Experimental research was a rare endeavor among the Greek elite, as was any form of manual labor, and Aristotle's untested speculations about the nature of nature were often erroneous. Furthermore, many of the early tools of science still had yet to be invented. There were no microscopes, no thermometers, no telescopes – not even a watch – and Greece was not fertile ground for the advancement of technology at that time as the slave-based economy kept the incentive low. Moreover, the procedures for experiment had not been invented. Aristotle was an observational scientist at best. But his approach to natural science was a great step beyond his predecessors, Plato and Socrates, who viewed true knowledge as obtainable only through the intuition of a well-trained mind.

Aristotle was weaned on definitions by Socrates through Plato. Although he did not imagine abstract definitions as real entities in the mystical way that Plato did, he recognized the need for clearly defined classes to which individuals could be assigned. By an unfortunate coincidence, Aristotle chose the human species as an example (Durant 1953; Cohen 1994) to demonstrate the mechanics of definition. As a result, he further solidified an aspect of the species myth by grounding it in what appeared to be the science of logic.

Using the example of "man" (i.e. *Homo sapiens*) as an object to be defined, Aristotle demonstrated that definition should be a two-part proposition. First, the object to be defined is assigned to a broader class, and Aristotle assigned "man" to the larger class of "animals." The second step is to add defining characters that will separate the object to be defined (in this case "man") as unique among all the other members of the

broader class (in this case, "animal"). In his example, Aristotle considered only one defining character was required – the adjective "rational." Thus, the two-part definition becomes *man is a rational animal*. With this short sentence, the concept of species was further mythologized (Veatch 1974; Berns 1976). Species in nature were now both definable classes as well as eternal entities.

Aristotle's greatest contribution may have been his creation of the science of logic, with its rules for definition and the syllogism, which grounded science in clarity and rationalism. But when misapplied, however, Aristotelian logic can be a misguided pursuit. The error in the usage of Aristotelian definition previously mentioned, combined with the method of syllogistic logic, instilled this faulty view of species with a façade of rationality that anchored it in myth. The syllogism's three parts (major premise, minor premise, and conclusion) are found in the commonly cited example: Man is a rational animal; Socrates is a man; therefore, Socrates is a rational animal. While the logic of the conclusion is inescapable, the validity of the major premise needs examination.

Aristotle believed the greatest good was to exercise rationality, and his grounding in reality led to exceptional scientific advances. He did dissections and his anatomical descriptions of animals were accurate. He classified animals by way of life, actions, or parts, grouping them into genera and species within 2 major groups – those with red blood, and those without (vertebrates and invertebrates, respectively). Under his student Theophrastus, whom he would name as his successor to head the Lyceum before he died, the field of taxonomy would reach a zenith which would not be surpassed until the Enlightenment with the work of John Ray and Carolus Linnaeus over a thousand years later.

Aristotle believed the universe had no beginning or end, and that change was cyclical (like the water cycle). He expanded the ideas of Empedocles (see below) which anticipated the concept of natural selection, saying our various traits arose spontaneously by chance, and those with groups of traits that were more fit would survive while those with less fit traits would not.

Aristotle's success as a scientist and his brilliance as a logician lent a weight of respectability and credibility to all his positions. This included his view of species as classes. As a result, this mistaken presumption regarding the foundation of biodiversity would eventually gain the level of dogma.

Non-Socratic views

Although the influence of Socrates, Plato, and Aristotle would hold court until the re-emergence of scientific thought after the Dark Ages, a number of other ancient philosophers provided glimmers of secular science after the Socratic philosophers had made their mark. Empedocles of Sicily (490-430BCE) was a contemporary of Socrates with very different views. He is the earliest known proponent of all matter being composed of four basic elements (fire, water, earth, and air) rather than merely one (Mayer 1950). Although inaccurate, this secular theory of matter was a positive step regarding the fundamental nature of the universe. He even hinted at the charges of molecules saying that the elements were controlled by two forces – love and strife (i.e. attraction and repulsion) and that the universe emerged through the interplay of these forces. He also postulated that all life emerged from the earth and that current organisms had evolved from past organisms through selection. He said that selection had eliminated

organisms that were unfit for survival or "furnished with sterile parts" (Fuller and McMurrin 1957). Yet he assumed that natural selection was no longer occurring – an understandable mistake given that the slow pace of evolution makes it rarely observable even though the evidence for it is.

Other theorists expanded and extended the ideas of Empedocles. Democritus of Thrace (450-370BCE) on the northern Aegean Sea was the first atomist, and as such he both enlarged and challenged the ideas of Empedocles. Democritus argued that there were different "atoms" in different types of matter, and that objects disintegrate when their atoms disperse (Fuller and McMurrin 1957; Serafini 1993). In his view, atoms and the void make up a universe without beginning or end. His student, Epicurus of Samos (341–270BCE) took another step towards a rational view of species by positing a universe in which atoms come together without intention or purpose (Mayer 1950).

Aristarchus of Samos (310-230BCE) was the first astronomer to propose heliocentrism, predating Copernicus by 1,800 years (Clagett 1955; Batten 1981). Although heliocentrism is not remotely related to species concepts, had this fact of cosmology gained traction during this early period in history, its establishment might have contributed to a body of knowledge that would have prevented the earth-centered and thus human-centered cosmic vision that became part and parcel of religious oppression.

Eratosthenes (275-195BCE) was a close friend of Archimedes and the second librarian to head the famous Library of Alexandria in Egypt (Clagett 1955). Established by one of Aristotle's protégés in the 3rd century BCE, this library was the ancient world's largest and it soon became the preeminent scientific research center and repository of

manuscripts. While working at the library, Eratosthenes recognized the earth's globular shape and measured its circumference, tilt, and size with surprising accuracy using geometric methods (Archibald 1949; Engels 1985; Rickey 1992).

Lucretius of Rome (94-49BCE) was an Epicurian atomist whose poem *On the Nature of Things* challenged superstition, saying reality is the result of the purposeless motions of atoms through empty space. He argued that death is nothingness, neither good nor bad, no different than the lack of existence before birth, and that "all things come to be without the aid of gods" (Jones 1969). He also said "Nothing in the body is made in order that we may use it. What happens to exist is the cause of its use," in a prophetic function-follows-form idea presaging Darwin's evolution by natural selection (Clagett 1955; Serafini 1993). He even suggested that the first living things formed from natural, stochastic processes based in atomic physics (Goodrum 2002).

These nascent ideas – secular hypotheses that might have sent humanity on a scientific path of dramatic discovery and achievement – were rent asunder by the accidents of history. The ideas of Pythagoras, galvanized by Plato, gained ascendancy instead. By dint of historical accident, the Platonic worldview would be adopted by the state of Rome through Plontius (Popkin et al. 1999) and Augustine of Hippo (Gilson 1955) in the early centuries of Common Era (CE). Augustine was instrumental in modifying and codifying Platonic philosophy in ways that would lend intellectual credence to Christian scriptural dogma.

The early Common Era

Pliny the Elder of (23-79CE) was a Roman historian, grammarian, and natural historian. His 37 volume *Natural History* cataloged information from some 2,000 other manuscripts (Serafini 1993). Much of what he documented was apocryphal, including animal-human hybrids. But Rome at this time was moving toward authoritarianism along with dogmatism in all areas, including science. Consequently, Pliny's catalog would be studied without challenge for hundreds of years, in spite of its inaccuracies. His view of fossilized sharks teeth as "tongue stones" that had no relationship to once living things would help erect a barrier to an accurate understanding of fossils for over a 1,500 years.

Claudius Ptolemy of Alexandria (90-168CE) wrote three major works (in astrology, geography, and astronomy) that also gained the status of authority. His astronomical treatise, the Almagest, entrenched the dogmatic but incorrect astronomical fact of geocentrism (Brotons 1995; Ruffin 1997).

Claudius Galen (129-200CE) became Rome's state physician and his ideas of medicine were also followed blindly for 1,300 years – ideas such as disease is the result of imbalanced "humors," the use of opposites are an effective way to treat disease, and a person's character can be deduced from his or her physique (Evans 1969). Galen was a bigoted classist who felt those that spoke any language other than Greek were, by definition, barbarians (Scarborough 1970). His human anatomy diagrams were inaccurate, based on pig and ape dissections because the state religion forbade the dissection of human corpses (Scarborough 1970).

Ptolemy and Galen epitomized the developing orthodoxy that would mark the Middle Ages – edicts handed down to be followed blindly. They became dogmatic icons

whose writings were authoritative, almost scriptural, texts that contributed to scientific stagnation rather than inspire scientific inquiry. This long period of stagnation left an imprint of validity on erroneous ideas, some of which continue to contribute to the unnecessary existence of the species problem.

Augustine of Hippo

Augustine of Hippo (354-430) was a disturbed, insecure, and fanatical (albeit effective) religious philosopher who incorporated and subsumed the philosophy of Plato into Christian doctrine. This synthesis was also personalized by his emotional responses to life experiences. With an acute sense of his own sinful nature, Augustine despised his desire for sex and abandoned his faithful concubine of 15 years along with their son in order to wed a wealthy woman of class. He described the weakness for sex he had been burdened with before his Christian conversion, saying he used to pray for "chastity and continence, but not yet!" (Outler 2006). He passed on this deeply personal sense of guilt and imperfection to countless generations of Christians by codifying it into his metaphysical version of Christian theology.

Rather than search for moral truths or empirical reality, Augustine created a metaphysical monument to his religious faith. Behind Plato's neutral perfect forms and rational good Augustine saw God. Ironically, both Plato (the self-assured rationalist from the upper class) and Augustine (the insecure and guilt-ridden religious fundamentalist from the lower middle class) abhorred change. They both believed reality was (or must be), at its core, immutable and eternal. In response to obvious change in the natural world, Plato forged a belief system founded on stasis, which he argued was more real

than the world itself. Without immutable forms, Plato felt, knowledge would not be possible (Keyt 1969). In Augustine's hands, Plato's ideal forms were refashioned as the perfection of God. He transformed the Platonic view of imperfect earthly creatures as poor facsimiles of ideal forms by attributing a lack of perfection to separation from God. Since Augustine believed that God created the world, he (like Aristotle) did not accept Plato's view that the products of ideal forms on this earth were merely illusions. Instead, he saw a dualistic, divided world with God utterly and infinitely different than creation. Augustine's God was pure goodness and pure reality while God's creations differed by degree in goodness and thus in reality.

This plagiaristic transformation of Plato's ideal forms fully mythologized Plato's static and definable species taxa by grounding them in spiritual authority and divine creation. This synthesis of classical philosophy and early Christian theology presented a powerful belief system that would hold sway until our intellectual emergence from the Middle Ages. And that emergence is only partially complete, given that this ancient synthesis still holds sway for many today. Although the scientific revolution to follow has opened up a world of discovery regarding biological evolution and the concepts of species, Augustine's mythology of species has not been fully abandoned – only modified.

The collapse of the Roman Empire

Hypatia of Alexandria (370 - 415) was one of the last scholars of Alexandria (Dzielska 1996). I include her in this discussion because her brutal murder at the hands of a Christian mob symbolized the dissolution of the Roman Empire and the beginning of

the Dark Ages – a period during which the development of science and evolutionary theory was effectively put on ice (Mayer 1950).

A brilliant scholar and a revered teacher, Hypatia had many students and she devoted herself to mathematics and astronomy. She epitomized learning, science, and independence of thought, and at the height of her powers may well have been the greatest living mathematician (Deakin 1994). But science had become increasingly identified with paganism, thanks to the Roman emperor Theodosius I, who made Christianity the official religion and promoted a policy of intolerance. Hypatia, who helped devise the astrolab (the main navigational instrument before the sextant) and the hydrometer (for measuring the specific gravity of liquids) was not one to kowtow to superstition. She is reported to have said, "Reserve your right to think, for even to think wrongly is better than not to think at all" and "To teach superstitions as truth is a most terrible thing" (Dzielska 1996). When bishop Cyril was promoted to archbishop of Alexandria, he encouraged brutal attacks on pagans, and prominent freethinkers became targets as they often do in religious pogroms (Deakin 1994). Hypatia's brilliance, popularity, gender, self-confidence, and willingness to challenge the church undoubtedly made her a prime target of Christian fundamentalists.

Within a hundred years of Hypatia's death, the breakdown of the Roman Empire was complete. Western Europe soon became a tapestry of rural villages ruled by tribal warlords and semi-nomadic people. Most scientific treatises, including the works of the ancient philosophers, were lost to Muslim conquerors (many of which were fortunately preserved by them and would become available again after the Middle Ages). The

Catholic Church was the only institution to survive, and little scientific progress would be made in the western world for nearly a thousand years (Jones 1969).

The Species Concept During The Middle Ages

Augustine's spiritual and intellectual journey transformed Platonism into Christian dogma, melding it into the state religion. This hybridized doctrine became the theological and philosophical status quo and remained in place and essentially unchanged for 800 years after the fall of Rome. Although this period was a long and difficult interval of cultural and scientific stagnation for western Europe, some changes did occur in both ideas and institutions. I shall refer to this time span plus an additional century or two as the Middle Ages, bracketed by the end of the Roman Empire sometime in the 5th century and the start of the Renaissance in the 15th century (Popkin et al. 1999).

By the end of the Middle Ages, Thomas Aquinas, like his predecessor Augustine, would again provide a new synthesis of philosophy and theology that was right for the time. But rather than coincide with a period of social chaos and anomie, this new synthesis would help usher in a era of intellectual rebirth and scientific discovery. It would lead to a reformulation of the mythological views of species in order to reconcile empirical discoveries with some old but deeply held precepts.

The collapse of the Roman Empire was a long and tortuous one, beginning with foreign invasions at the end of the 4th century lasting many years (Jones 1969). A highly developed civilization was slowly wiped out by relatively primitive conquerors – nomads with neither a well-developed judicial system nor urban economic and social systems. As a result, the Empire's civil society disintegrated, along with its roads, commerce, and

industries. What remained were small, isolated, agrarian hamlets of people struggling to survive from year to year (Durant 1953; Jones 1969).

Most of the works of the ancient philosophers and scholars were lost to the west at this time. People in the region lost both the art of writing and reading. Literacy was rare even among the ruling elite (Jones 1969). During these Dark Ages, the Christian Church was about the only institution to survive. In fact it thrived, since during such desperate times salvation after death gained primary importance – and the Church was nearly the only game in town (Fuller and McMurrin 1957). By the 8th century, Papal supremacy furthered the Christian cause by centralizing the Church's authority. As kings and other rulers found it politically useful to convert, they two came under the authority of the Church.

A second cultural aspect of Christianity also contributed to its survival. Numerous monastic sects emerged that, rather than vying for power and rendering unto Caesar, withdrew from the world to render unto God (Jones 1969). In the harsh climates of Europe, monasteries were places where the devout could band together for communal survival. Benedict of Nursia founded 12 monastic communities in the 6th century that provided the model for Monasticism based on humility and discipline.

During this long period of academic and civil stagnation, the ontology of species was not a concern, as the difficulties of survival did not allow many opportunities for scholarship. Augustinian precepts were taken for granted without challenge, and the mythology of species gained prominence from sheer duration. The image of species fixity was becoming a millennial belief, supported in documents by the giants of the human intellect and subsumed within the Christian theology of creation and perfection.

The inertia of this multi-layered mythology would eventually withstand a wealth of scientific discoveries that would emerge at the dawn of the Enlightenment and it would hold until Darwin and his supporters finally began to successfully unravel the details of species change.

As the Roman Empire collapsed, the absence of a central government led communities to rely on men of property for leadership (Jones 1969). Many landowners had already been delegated the power by titular emperors or local regents to collect taxes, and the loss of a centralized power often left them in control of their own provinces. A number of fiefdoms emerged from the former domain of the empire, and farmers in these regions gave up their independence for protection. Many of the warrior leaders of invading tribes gained provinces as well, and their soldier citizens remained under their command. These various rulers considered themselves kings, and the separate kingdoms became divided into feudalities of lesser and lesser size, with rulers of lesser and lesser stature, all pledged in a hierarchy of service to those above them.

Survival was a matter of loyalty to one's immediate overlord. Status replaced citizenship, and heredity became the broker of power. The local rulers were left to their own devices as long as they successfully proffered their feudal taxes and oaths of allegiance up the chain. Dukes, counts, barons, and knights all claimed some authority, and wars of acquisition were frequent.

And so the western world remained a primitive place of relative stagnation for centuries until finally the locus of power began to shift. Commoners gained wealth through creativity and trade, and urban culture began a revival (Jones 1969). Small cities developed that would one day supplant feudal manors. As life improved, the view of a

hostile world with an afterlife as the only opportunity for salvation began to be replaced by an earthly world of promise and achievement. The entrenched idea of species stasis would soon be challenged as opportunities to pursue the art of science finally became available again.

In the 12th century, the works of Aristotle again became available to the west (Serafini 1993), helping to stir the people's imagination and awaken the relative slumber of stagnant, medieval scholarship. Aristotle's contributions to the scientific method were again new to the west, opening the natural world up to discovery in new ways. But it would take time to gain competence in the use of empirical methods to study the natural world and its biodiversity. Still, the act of experimentation was taking its first halting steps, and change was in the wind.

The medieval schools of churches and monasteries began to swell with students during this period of intellectual awakening (Jones 1969). Eventually these institutions developed rules, organized curricula, and codified qualifications for degrees. The degrees were at first to qualify scholars as teachers, but the guilds of scholars began to specialize, offering degrees in theology, law, medicine, and the arts, and the first western university appeared in the 12th century (Serafini 1993).

Philosophy during the Middle Ages was essentially Augustine's version of Platonism, with God as the ideal form of good. With the re-emergence of Aristotelian metaphysics, logic, and empiricism, a new synthesis was needed to prevent Christianity from plunging into secular, Neoplatonic heresy. Thanks to the Augustinian synthesis, Plato's ideal forms still resonated, especially within the Church. If each person had a separate reality (unassociated with an ideal form), the concept of original sin staining all

people would be difficult to grasp. But a sinful universal man could explain original sin for all, including all people to come. Carried to its extreme, however, these universal forms are more real than particulars, forming a hierarchy of successively more general, and more real, universals, until one reaches the ultimate reality of God. Such a metaphysical system, with God enveloping everything in a hierarchy of reality, appeared to give credence to pantheism – with the physical universe as a manifestation of God (Jones 1969). Creatures could then be identified as parts, however small, of God – a heretical perspective that, in the view of Church authorities, opened the door to human pride. Thomas Aquinas would provide a new synthesis of rationalism and religion to manage this metaphysical crisis.

Thomas Aquinas and the new synthesis

Thomas Aquinas (1225-1274) merged Aristotelian philosophy with Christian theology in a synthesis that was right for the society that was emerging from the Middle Ages. Aristotle had accepted the reality of Plato's perfect, ideal forms, but unlike Plato (who considered the forms independent), Aristotle saw them as inextricably bound to – actually embedded within – their particular, physical instances on earth (Mayer 1950; Jones 1969). Considering the particular instances as real (although less than perfect), Aristotle felt examining them would offer insights into perfection – creating a powerful incentive for conducting empirical science. But Aristotelian naturalism held that the world was eternal and did not come into being by an act of creation. By his definition, the world was always there. In response to this heretical view, authorities in Paris began banning Aristotle's works in 1210 (Jones 1969).

Thomas Aquinas saw much in the philosophy of Aristotle to be admired (Mayer 1950; Popkin et al. 1999). But unlike Aristotle, he considered the relationship of particulars to perfection as aspects of God's divine plan. In his view, all creatures and things on earth have the ultimate goal of returning to God – of being perfected by Grace – even though they have short-range goals here on earth as well (Jones 1969). Since Aristotle (and many of the ancient Greek philosophers) pursued ethics as secularists, Aquinas would have to modify Aristotelian metaphysics (as Augustine did with Platonic philosophy) in accordance with his belief in God.

Aquinas viewed morality and goodness as measures of connectedness to God, while immorality and evil were demonstrations of separation from God. He realized that the Christian theology of his day, which clashed so strikingly with classical scholarship, needed supplementation (Jones 1969). To the Greeks, humans were (at their best) the pinnacle of existence and reality, the ultimate creation. For Christians, mortal humans were helpless, depraved, and sinful. Aquinas needed a formula to merge these discordant secular and Christian worldviews. He developed one, and expanded it to a philosophy of science.

Although similar to the ideas in the Augustinian synthesis, Aquinas's approach offered a progressive new twist. Without resorting to the harsh dualism of Augustine, Aquinas argued that philosophy manages things that can be proved empirically, while religion deals with that which requires faith. He did so by dividing theology into revealed and natural truths, with the latter being susceptible to proof (Jones 1969). This creative and respectful separation of philosophy and religion provided a non-combative and profitable worldview long before Gould's formulation of "non-overlapping

magisterial" (Jones 1969; Gould 1997). Aquinas referred to this as natural theology, and in so doing opened the door to research by devout Christians, an act that would kick-start a revolution in science during the Enlightenment.

In the natural theology of Thomas Aquinas, revelation would not contradict reason, but instead supplement it. As he put it, "Grace does not destroy nature, but perfects it," adding that "reason should minister to faith..." (Jones 1969). Aristotle was his guide to perfecting theology and resolving the controversies between faith and reason. Like Aristotle, Aquinas viewed the universe as a collection of particulars that emerge from both matter and their embedded ideal forms. In contrast to Augustine's harsh dualism that demonized nature, Aquinas saw all aspects of the universe as a single, unified hierarchy. Yet he escaped the criticism of pantheism by defining God uniquely as the one Creator, which we creatures can never be (Mayer 1950). This approach gave the cosmos a unified, rather than dualistic, structure.

Aquinas accepted Aristotle's view that we humans are natural beings, but he argued that this description was incomplete. Each of us is also a child of God, with the higher goals of loyalty and obedience to God (Jones 1969). Thus, to fully comprehend reality, these two separate aspects of the human condition are necessary. This wedding of rationality to theology helped dissolve the domination of orthodoxy and catalyze a tempo of change that would bring the intellectual stagnation of the Medieval period to an close. Although "Thomism" would become official Church doctrine, thus shifting it from a progressive philosophy to the conservatism of the status quo, its acquiescence to free thought would be the agent of its own undoing. Within a few centuries, Thomism would largely be overthrown (Crombie 1967). Aquinas's philosophical offspring were the

natural theologians who emerged during the Age of Reason to pave a road to the Darwinian revolution with their fascination for, and careful observations of, nature.

The syncretic creation of Thomas Aquinas extended and fortified the continuous thread of the myth of species fixity. Through all the philosophical and theological changes during a period that spanned more than a thousand years, the mythology of species fixity had been a constant. It emerged from the cultish concepts of Pythagorean mysticism and gained broad acceptance through Plato's repackaging for broader appeal some 200 years later. Each synthetic incarnation of the Pythagorean conception of perfection and permanence behind all things (by Plato, Aristotle, Augustine, and Thomas Aquinas) maintained the founding principle of species fixity across a vast stretch of human history, etching it as a normative viewpoint across time and cultures.

The mythical aspect of the species problem is grounded in the establishment of species taxa as classes rather than individuals. Most myths have a temporal requirement for belief – the time required to be passed down from one generation to another, while being imbued with spirituality and endorsed by the ruling elite – and species as classes surely qualify. The cultural institutions within society are girded by myths that found those institutions in universal truths. The authority wielded by the three fields of philosophy, religion, and natural science, all having associated species with ideal forms over so long a period of time, has created a mythical class association to taxa that is not easily discarded and is instead often held without conscious recognition.

The legacy of Thomas Aquinas in religious circles was so vaunted that he ascended to sainthood within 50 years of this death. But his impact on the worldly pursuits of science and education are equally illustrious. By making it possible to study nature without being condemned for heresy, Thomas Aquinas's fortuitous merging of Greek philosophy and rationalism with Christian doctrine launched a revolution in scientific inquiry. Natural theology is the demonstration of God's existence through the illumination of Creation via scientific research rather than inspired revelation or biblical scholarship. The creation of species was viewed as God's inspiration, and after Aquinas removed the barriers to the scientific examination of creation's details, natural theologians put their own stamp on species fixity – an axiom that had already spanned a thousand years.

The philosophical origins of natural theology are found, in part, in the works of Plato, who suggested the reality of the gods can be ascertained rationally. But Plato's science was contemplative rather than hands-on, so the discipline did not emerge as a force with which to be reckoned until the Middle Ages were nearing an end, and the practice of natural theology clearly helped bring this period of western intellectual stagnation to a close.

Two scholars helped propel the study of natural science at the end of the Middle Ages. The first was Roger Bacon (1214 – 1294) – an English Franciscan monk who had the good fortune to be an acquaintance of Cardinal Guy le Gros de Foulques. In 1265, Bacon was asked by his friend – now Pope Clement IV – to write to him concerning

philosophy within theology. Bacon was uniquely qualified in both religion and science, and he responded with his *Opus Majus*. Like Thomas Aquinas, Bacon felt science and many of the ideas of Aristotle could be incorporated into theology (Jones 1969). Furthermore, he promoted the scientific method and urged theologians to reject blind obedience and study science.

The second medieval philosopher to promote science and help bring the Middle Ages to a close was William of Ockham (1288 – 1348). He too was a Franciscan, and although not a true natural theologian, he promoted rational science and was staunchly religious. William denied the existence of ideal forms, arguing they were merely human ideas without any extra-mental existence (Tornay 1936). This makes sense, given his famous edict to avoid creating unnecessarily complex explanations without firm evidence. He also differed with the precept of natural theology that God could be understood through the study of nature. He felt an understanding of God could only be gained through faith and divine revelation. Still, his promotion of scientific research opened the door a bit further to the Renaissance and the Age of Reason.

By the 16th century, the stranglehold of the ancient masters was being loosened and the Renaissance was in full swing. Although there was still a risk of condemnation for heresy by Church authorities, a number of pioneering scientists pushed the limits of that risk to advance research. Like Aquinas and Ockham before them, most were devout Christians working within the precepts of natural theology, widening the opening for scientific advancement. Brief accounts of some of those devoutly religious scientists will help demonstrate the course of the revolution in science that emerged as a result of the natural theology movement. Their work would lead inexorably towards the theory of

evolution and an understanding of species change. Yet the dogma of species fixity would persist even while old ideas were toppling in the fields of medicine, cosmology, physics, and geology. Species fixity was so deeply rooted in western philosophy and creation myths that it held the field of biology back while the other fields leapt forward (Hull 1965a). Ironically, the survival of this erroneous concept during a period of great scientific advancement lent the ancient idea new credibility, prolonging its life even longer.

Andreas Vesalius (1514 – 1564), a Flemish anatomist and university instructor who did his own human dissections was rewriting the texts on human anatomy, and toppling Claudius Galen from his millennial perch of authority. Vesalius's 1543 *De Humani Corporis Favrica* made human anatomy a modern science and he launched the new science of comparative anatomy. Although not a natural theologian, his texts replaced those of the old masters in university curricula, advancing empirical science.

During this revolutionary time of change in science, other scholarly fields were swept up in this intellectual movement, with advances in each propelling the others. The lawyer and philosopher Francis Bacon (1561 – 1626) promoted empirical research and further refined the inductive methodology of science. He too was a fledgling natural theologian, saying, "a little philosophy inclineth man's mind to atheism; but depth in philosophy bringeth men's minds about to religion" (Sahakian and Sahakian 1993). Although his polemics may have provided a striking sound-bite in his day, his contributions to greater philosophical depth, in concert with empirical research, would eventually help remove species from the supernatural realm of religion and demonstrate the fallacy of the species myth.

Galileo Galilei (1564 – 1642), a deeply religious man who never rejected his faith and was dedicated to the church, codified laws of motion and provided hard evidence for Copernican heliocentrism (Wisan 1986). Galileo had the hallmark traits of the natural theologians to come – strict adherence to empirical science and deep religious faith, which he combined without obvious conflict. Although Galileo's house arrest for his promotion of the Copernican system of heliocentricity is well known, even the Inquisitors of Rome had by this time allowed the hypothesis to be discussed – just not advocated. Although a seemingly small opening, free thought is difficult to control, and the door to free inquiry would only open wider after Galileo (Thomson 2005).

Robert Boyle (1627-1691) was arguably one of the first truly modern scientists and was considered one of the most brilliant scientists of his era (Thomson 2005). This Irish scientist lifted the field of chemistry up from its alchemist foundations by employing strict scientific methodology. He was also a devout Christian who considered atheism to be a myth and viewed scientific research as a religious duty (Thomson 2005).

John Ray (1628-1705) was both priest and biologist and represented the quintessential natural theologian who promoted the nobility and sanctity of science while conducting groundbreaking research (he proved living wood conducts water and did important early work in taxonomy, inspiring future systematists). While a student at Trinity College in England, he wrote a scholarly flora of the plants of Cambridge. He was a brilliant student who rose rapidly after graduation to become Junior Dean, and then in 1660 was ordained a priest. But Ray was a freethinker as well, and was defrocked in 1662 for refusing to submit to a Uniformity Act that required submission to very specific Anglican rules. Thereby freed from his priestly duties, he made natural history his career

path and spent the rest of his life collecting, doing research, and writing, becoming Europe's preeminent natural historian (McMahon 2000).

After traveling throughout Europe collecting specimens and discussing science with the other top naturalists of his day, Ray recognized the critical need for an organizational system to categorize the ever-increasing collections of different organisms – a system by which one might discern deeper insights into creation. It was Ray's system of organization that labeled "kinds" as "species" and began the profession of systematics (Jauhar and Joshi 1970). In so doing, Ray etched even more deeply into the human consciousness the concept of species fixity. A classification system needs discernible entities to classify, and this suggests their inherent discreteness. Once those classifications have been made, with rules of identification and names for each species cataloged, the process of classification itself begets conceptual fixity. As new specimens come in, the format for classification awaits them, and the presumption is that all are classifiable.

As his health deteriorated, Ray spent his later years writing books on science and theology. His 1691 book, *The Wisdom of God Manifested in the Works of the Creation*, would become the original manual of natural theology. In it he took the idea of natural theology and filled it in with examples he felt provided evidence of God's perfection. As he put it, "the works of this visible world… [are] demonstrative proof of the unlimited extent of the Creator's skill, and the fecundity of his wisdom and power" (Clayton et al. 2006).

In light of the historical value of John Ray's seminal work on natural theology, along with the power of his writing, I must digress a while on this one piece. The fact

that the term "species" (rather than "kind" or some other term) is thoroughly established in the biological lexicon establishes the significance of Ray's book. Ironically, just as William Paley's tome on natural theology would later contribute to Darwin's own developing theory of evolution (which would end all serious attachment to natural theology as a credible scientific framework), Ray's publication must have been an important stimulus for the production of research that would eventually dismantle the premises undergirding natural theology.

Ray might be considered the true father of natural theology with his treatise providing the ontological tenets for this noble occupation. His view that total morphology should be utilized in delimiting species anticipated taxonomic methods 100 years before the work of Linnaeus (whose approach was considerably more limited). Ray's strict adherence to empirical science caused him some grief, as he came to recognize fossils as once living, causing him to question earth's scriptural age as well as the permanence of species (Arber 1943).

Fellow natural theologian and contemporary of John Ray, Nicholas Steno (1638-1686) was a Danish researcher who pushed science ahead in numerous fields, including anatomy (he showed mathematically that muscles changed shape but not volume) and paleontology (he recognized Pliny's tongue stones as fossil shark teeth replaced by minerals) (Cutler 2003). His most lasting contribution was to geology (Laudan 1994). In his 1669 *Prodromus* he proposed the *Law of Superposition* (that horizontal layers of rock and soil once were fluid lava and sediments that were laid down newer above older). This simple principle modernized the fields of paleontology and geology, suggested an earth of great age, and provided a cosmic view that would one day lead to a new view of

species. Born a Lutheran, Steno was ordained a Catholic priest and eventually made bishop, spending his last years as a missionary. But his landmark theory of superposition showed the fossil record as a chronology of different time periods occupied by different creatures, which would pave the way to Darwin's discovery.

The English researcher Robert Hooke assisted Boyle in his lab. He was considered Boyle's intellectual equal, and helped propel the field of chemistry forward with his complementary talents in math and physics. Although no natural theologian, Hooke's contributions to the advances made by Boyle's lab were substantial, thus contributing to the influence of Boyle (who gained much wider recognition, probably due to his patrician background).

Even Isaac Newton (1642-1727), the paramount figure in empirical research and the elucidation of natural laws (universal gravitation, light's color spectrum, calculus, and the 3 laws of motion) was a devout Christian and consummate natural theologian. As he put it, "Gravity explains the motions of the planets, but it cannot explain who set the planets in motion. God governs all things and knows all that is or can be done." Although his scientific accomplishments seem difficult to compress into a single human lifetime, Newton's theological works were even more extensive (Cohen 1960). His scientific discoveries would provide evidence for a universe that runs itself with a preciseness and predictability that hinted at divine perfection. So he contributed to natural theology by demonstrating the apparent perfection in the universe, created (he felt) by a divine designer who employed universal laws that can be discovered. Yet his findings also contributed to a rationalist view of the universe that does not require a supernatural guiding hand.

The burgeoning of natural theology coincided with dramatic expansion in the sciences and technology, encouraging exploration and colonial expansion. Scientists went along on many of these expeditions, returning with a wealth of biological specimens. Carolus Linnaeus (1707-1778) the Swedish physician, botanist, and pioneering taxonomist, documented his collections and those of his students in his *Systema Naturae* which he began in 1735 (Linné 1758).

Linnaeus system of nomenclature and classification was based on shared traits. His use of number and arrangement of reproductive organs for plant classification (with stamens determining the taxonomic rank of class, and pistils determining the rank of order) produced some odd groupings (e.g. conifers with castor beans). This bold approach put humans, orangutans, and chimps in same genus, and in the family Primata with simians and lemurs. Yet the concept of unguided evolution never occurred to him.

The Scottish geologist and natural theologian James Hutton (1726-1797) was personally responsible for expanding the earth's age through his uniformitarian and plutonist theories. After repeatedly observing that granite often penetrated metamorphic schists, and that Steno's geological layers were often vertical rather than horizontal, Hutton proposed sequential cycles of deposition, uplift, and erosion over dramatically long periods of time in his in 2 volume *Theory of the Earth*. Like Linnaeus, he saw too much to view species as hard and fast, and recognized a level of change in species that might be due to competition. Yet, given his religious piety, he, like all natural theologians, presumed the levels of change could only occur within species, rather than lead to new ones.

Thomas Malthus (1776-1834) was an Anglican minister and Cambridge mathematician whose *Essay on the Principle of Population Growth* recognized that geometric population increases resulted in extreme competition for limited resources and that as a result, cruel mechanisms (i.e. starvation, disease, and war) kept population numbers in check. Although his ideas contributed to evolutionary theory and non-static concepts of species, Malthus was a devout Christian who opposed Darwin's theory.

Boyle, Ray, Steno, Newton, Linnaeus, Hutton, and Malthus were all creative scientists who viewed research as a window to Creation. Their careful and productive pursuit of understanding God's creation gave natural theology a legitimacy that catapulted science forward. During this time, the concept of species remained relatively secure in its static form. But natural theologians advanced science so much in the process of pursuing the details of divine creation that they also became the authors of the early works that would eventually contravene the tenets of natural theology. Their exacting research and extensive data collection provided the information about biodiversity that would lead to the theories of evolution and bring an end to the concept of species as static entities.

William Paley (1743-1805) was an Anglican Bishop, philosopher, and Christian apologist. Unlike the natural theologians who preceded him, Bishop Paley was not a scientist, and this difference coincidentally heralded the end of natural theology as a profession of high esteem. Most practitioners after Paley and up to the present have had neither the scientific credentials nor the professional status of those that came before him. The movement of natural theology shifted from one of scientific professionalism to pseudoscientific dogmatism with practitioners more interested in bringing the discoveries

of science into compliance with Biblical tradition than in doing scientific research themselves.

The freedoms that enabled natural theology to blossom also allowed the emergence of challenging new ideas in philosophy and epistemology. Paley's impetus to writing *Natural Theology* was mainly a response to the Epicurean atomism that challenged the precepts of Christian doctrine. His treatise was so well written and so well argued, that it was in its day a true best seller, and its influence was pervasive. Charles Darwin found it very intellectually stimulating and wholly believable. Ironically, Paley's impact on Darwin would later impel Darwin's research into evolution, the results of which would doom natural theology to scientific obscurity. Although no clear theory of evolution had been articulated with evidence to support it in Paley's day, the idea had been bandied about since ancient times.

The beauty of William Paley's work is that it provides an argument for a view of nature and science that fits an optimistic view of the world. This easy-to-grasp outlook imbues the world with positive meaning and direction. But clearly it is an attempt to hang on to a view of species as static by adding an emotional content that has kept it in the general consciousness. Although Charles Darwin would soon change the intellectual landscape with his evidence of an evolutionary mechanism that elevated the discipline above the stochastically infeasible Epicurean atomism, the emotional appeal of Paley's view has successfully prolonged the life of static species concept and species taxa as classes.

FROM DARWIN TO THE PRESENT

The superb science and discoveries made by natural theologians had accumulated to a point in the mid 19th century that many of the old ideas based on religious dogma were straining at their leashes. Clearly the earth was far older than the 6000 years since the beginning of the Biblical creation. Fossils were now recognized as evidence of extinct species, and the stratigraphic geological and paleontological data strongly suggested that not all species had come into being at the moment of creation. Charles Darwin, originally a natural theologian himself, took his trip on the HMS Beagle at a propitious time in history. He was well prepared to study biodiversity, he had read or would soon read the important ideas in related fields of science, he was about to embark on a world-wide voyage of scientific discovery, and he had no axe to grind (he himself accepted the tenets of natural theology at the time he boarded the Beagle).

Although the proponents of biological evolution were still at the disadvantage of having yet to clearly identify a functional evolutionary mechanism with the evidence to support it, the dramatic variation and sheer numbers of species was becoming so great that it was becoming more and more difficult to explain biodiversity without such a theory.

Darwin provided both the mechanism of natural selection and the evidence to support his more complete theory that evolution of species had occurred and continues to do so (Darwin 1859). His success in this regard was made apparent by the rapid acceptance by those in the biological sciences. T. H. Huxley recalled being so struck by the simplicity and rationality of Darwin's arguments that it freed him, and most of his

contemporaries concerned with natural history, from the dilemma of choosing from long-propounded teleological explanations and insufficiently supported evolutionary hypotheses. As he put it, "How extremely stupid of me not to have thought of that" (Durant 2000).

Even with the rapid acceptance of his theory of species evolution, there was contentious debate regarding the process of speciation, and subsequently disparate views of species themselves. Darwin considered the process to be exceedingly gradual, and he had his supporters. But others considered the occurrence of speciation to be dramatically sudden, in a process referred to as saltation. Thus, even though his revolutionary theory provided a rational basis for the unguided evolution of species, it led to the first of many real species problems.

Before Darwin published his *Origin*, theories of species evolution had been batted about by a few respected names in science, including Georges-Louis Leclerc, marine biologist Robert Grant, Darwin's grandfather Erasmus Darwin, Jean-Babtiste Lamarck, Robert Chambers, and Geoffroy Saint-Hilaire. Those theories, however, had never gained serious consideration by the wider scientific community (Provine 1982; Richards 1992). It was initially an affront to the more respectable science of natural theology whose roots extended deep into the rich soils of ancient Greek philosophy. But so much evidence had been gathered suggesting species had been changing over time that when Darwin presented such a powerful case in 1859, scientists quickly began to find ways to accept biological evolution. But they still had to couch it in the myths that were entrenched in Western philosophy (Provine 1982).

Since most failed to grasp natural selection, they still assumed God was doing the selecting (or some other directed force driving species towards complexity), so design held (Provine 1982). With the recognition of species change and an ancient earth, many natural theologians managed to modify their beliefs, accepting that species had come into existence after creation – but still by divine design rather than evolution. Richard Owen, the well-known paleontologist and comparative anatomist, argued that new species came into being spontaneously from pre-existing species via "creative energy."

Some of Darwin's biggest supporters promoted his secular theory but challenged the details. Darwin saw what he called the transmutation of species to be very slow evolutionary change, and this would suggest that transitional forms would be apparent in the fossil record. Although Thomas Henry Huxley and Francis Galton both defended Darwin's views and accepted the role of selection, they argued against Darwin's idea of gradual transmutation. They both defended the idea of evolution by saltationism – dramatic mutations creating decisively different organisms. They both believed that the gaps in the fossil record supported their saltationist view (Provine 1971).

Before Darwin had published *Origin*, Lyell had helped convince Huxley that gaps in the fossil record supported the sudden appearance of new species. Darwin's theory of the gradual transmutation of species simply defied the evidence, and Huxley held this belief all his life in spite of his proud position as "Darwin's bulldog."

So although natural theologians held on to their shared belief in the involvement of God's designing hand, and Darwin's supporters promoted natural selection over an intelligent designer, some in both groups now accepted evolutionary change. But unlike Darwin, they believed evolutionary change to be sudden and obvious, establishing a new

species that would then be stable and definable. T. H. Huxley lumped species in with higher taxa as stable classes, arguing, "The fixity and definite limitation of species, genera, and larger groups appear to me to be perfectly consistent with the theory of transmutation. In other words, I think transmutation may take place without transition" (Huxley 1900), by which he meant there were no transitional or intermediate steps in the emergence of new species.

Darwin was not convinced because he thought "sports" (the offspring of domestic animals with strikingly evident phenotypic changes) occurred too rarely to provide the variation required for speciation, and most sports were infertile (Darwin 1859; Burkhardt et al. 1997; Stamos 2007). The dramatic traits of those that were fertile were soon swamped and lost after a few generations. But Huxley argued that the very nature of their "monstrosity" suggests a strength that would enable those changes to continue in later generations (Provine 1971).

Evolution had gained new respectability and broad recognition. But with Darwin's most admiring supporters debating the most important details of his theory, and nearly everyone still viewing species as fixed classes (although with new ones occasionally evolving and some going extinct), the age-old myth of species stasis was still intact, if not a bit tattered around the edges.

Like Huxley, Francis Galton shared Darwin's belief in the evolution of species, and that all life has a common ancestry (Galton 1869). Also like Huxley, Galton opposed Darwin's view of evolutionary change by what he termed "insensible gradations." He developed a theory of regression towards the mean in which the natural variation in a population reaches an equilibrium, making the selection of "mere variations" ineffective

(Provine 1971). He described a rough stone as analogous to species, with numerous facets, all of which were opportunities for change. But as long as it rested stably on one facet, it remained the same. The minor changes of Darwin's gradual evolution might temporarily jostle the stone, but it would return to the same facet and resume its stability. To actually move to a different facet, thus creating a new species, required a powerful force in order to "overpass the limits of the facet on which it has hitherto found rest" and reach "a new position of stability..." Thus Galton's "positions of stable equilibrium" remind us that even with the new definition of evolution by natural selection, species were still viewed as definable classes among secular scientists. As inaccurate as Galton's theory of stable equilibrium turned out to be, and perhaps because of its seductive imagery, Galton helped launch population genetics which would ultimately lead to the Modern Synthesis and great advances in understanding the mechanics of evolution. In his day, however, species concepts remained shackled to Plato's metaphysics and Augustine's theology. The new openness to science, made possible by Aquinas and his natural theologian offspring, only enhanced – and gave credence to – the acceptance of species as largely fixed and definable.

At the time of Darwin's death in 1882, hundreds of articles on evolution had been written in response to his theory (Provine 1982). Although biological evolution had become an accepted scientific theory, the vast majority of biologists opposed the mechanism of natural selection, and by the turn of the century, Darwin's view of gradual evolution was largely rejected.

In 1900, Hugo De Vries rediscovered Mendel's research while studying *Oenothera* hybridization and recognized Mendel's particulates as his newly coined

"pangenes." In response to findings of Mendel's research, the saltationists argued mutations provided the mechanism for sudden evolutionary leaps, and De Vries' mutation theory posited speciation could occur in a single jump.

Darwin had had his supporters before Mendel's work was rediscovered, including Karl Pearson and W. F. R. Weldon. Afterwards, these proponents of slow, incremental evolution became known as biometricians, and were opposed by the Mendelians who promoted saltationism, launching the species problem in earnest. The debate was not simply between those slow or unwilling to accept the revolutionary but well supported theory of evolution that overturned the long-held belief in species fixity. Now the species problem was a post-Darwinian debate between evolutionary biologists.

Karl Pearson was a math professor who met the biologist Walter Weldon. Weldon needed statistical techniques beyond what he had learned from Galton for his biological questions, and that launched both their careers as biometricians. Pearson would develop statistical tools (linear regression and correlation, classification of probability distributions, his chi-square test, etc.) that launched the field of population genetics. At this point, William Bateson parted ways with Weldon and Pearson and the two camps were set. Weldon and Pearson – the biometricians, supported evolution by natural selection of small, incremental changes, while Bateson and the Mendelians supported discontinuous evolution via sudden leaps.

Species concepts and the Modern Synthesis

The Modern Synthesis had wide support through the 40s and 50s. This more thorough view of evolution added the mechanisms of drift and gene flow to natural

selection. The two most influential publications were Dobzhansky's 1937 *Genetics and the Origin of Species* and Mayr's 1942 *Systematics and the Origin of Species*. At the inception of the Modern Synthesis there was a confidence about the species concept, but that confidence was to be short-lived.

Dobzhansky recognized species as discrete groups "encountered among animals as well as plants, in those that are structurally simple as well as in those that are very complex. Formation of discrete groups is so nearly universal that it must be regarded as a fundamental characteristic of organic diversity" (Dobzhansky 1937). Mayr (1942) defined the biological species concept (BSC) as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." Although the BSC soon became (and has remained) the most influential species concept, it was quickly challenged, and numerous new concepts would compete with it for primacy (de Queiroz 2005).

Mayr (1942) commented on the paradox that most taxonomists at that time, although they recognized evolution, still held static views of species taxa. In those days, taxonomists were holding evolutionary biologists back. Taxonomy was, after all, a classification system and organizational means to an end. Decades later it would, in its incarnation as phylogenetic systematics, become the cutting edge of evolutionary biology. But by the 1940s after decades of research supporting evolutionary theory, the myth of species stasis remained a cultural phenomenon that prevented a broad recognition of species as dynamic, evolving individuals. Furthermore, Mayr mentions that taxonomists within different specialties, from bacteria to mammals, had developed complex

terminologies specific to the groups of organisms they studied. Thus the species problem was being enlarged with disparate approaches to taxa.

A debate between Ernst Mayr and the paleontologist Benjamin Burma (Burma 1949; Mayr 1949a, 1949b) demonstrates the difficulty of preventing a clear recognition of species from becoming muddled. Burma argued that species were fictional constructs (rather than real entities) on a continuum that can only be divided arbitrarily, and they are always changing. As he put it, "species and subspecies ... are merely convenient labels for arbitrary groupings and have only a minimum of biological meaning." It appears Burma was approaching the concept of species as individuals, as he described individual organisms as indefinable as well, due to their constant change. He even argued that a hypothetical individual organism named John is never the same from one moment to the next. He identified John the zygote as $John_0$, and the first division as $John_1$ and so on. "Now he is $John_{1324}$; the next instant he is $John_{1325}$, forever and irrevocably different from any John that has come before or from any that will come in the future. Thus John is a succession of conformations of matter in time, and any meaningful study of him will have to consider the four-dimensional $John_{0+1+2+3+4+...n}$." So Burma recognized the reality of species as indefinable (with "John" as a species analog), as is the case with any individual. But he failed to value species as individuals, missing the significance of his own analogy, arguing instead that, "When we try to deal with larger aggregates of individuals, our categories become more and more abstract and empty of all real meaning." Burma took the view that species taxa were practical organizational tools without discrete reality. He felt that if unbounded temporally, there would be continuity back to an original primordial cell, making a single species composed of all present and

past organisms. He argued the alternative view – of a species as a series of breeding populations at a moment in time – would present us with an infinite number of species, "time being infinitely divisible." Since any bracketed period of time, however short or long, would be an arbitrary decision, species were, for Burma, simply unreal abstractions.

Mayr replied to Burma that each species is sharply separated from every other into well-defined units (Mayr 1949b). Although he agreed that breeding populations may differ from one moment to the next in a variety of details, he argued there would be little difficulty in identifying and separating the breeding populations of two different species, even sympatric ones. Mayr strongly emphasized that the reproductive barrier was the critical factor in his retort to Burma. Regardless of how diverse individual organisms may be (by gender, degree of morphological variation, life stage – from zygote to adult – etc.), if they are part of a cohesive interbreeding population, they are, Mayr argued, members of the same species. Furthermore, he felt that the relational differences between sympatric species clearly define each as a separate cohesive unit, regardless of the potential for variability within any one species from moment to moment.

Burma's take on species is particularly instructive. It is not easy to jettison the multi-millennial myth of species taxa as a classes of organisms. But once one recognizes the implications of evolution, this must be done. But then what does one have? If a species taxon is not a class whose members are definable by the necessary and sufficient traits that identify the class, then a species cannot be defined. Burma's analogy of the indefinable organism brought him right to the doorstep of individuality. Why did he fail to step through? I think it is because we are unaccustomed to viewing a loose set of organisms as parts of an individual.

Even though the parts of an organism are constantly being worn out, lost, and replaced in the same way that the parts of a species (i.e. the organisms within a species) are lost and replaced, the ontological reality of species taxa as individuals is not intuitive. This difficulty is at the heart of the species problem. The lag time between recognizing the elements of biological evolution and subsequently jettisoning the ancient view of species as classes has led to a kind of malaise. God and the security of perfection, with a hierarchy of fixed taxa formed at the moment of creation, had finally given way to the messy reality of imperfect species evolving by chance mutations and drift along with local selection. Few were capable of recognizing species taxa for what they were – cohesive populations on their own evolutionary paths. Thus the species problem remained very real after the rejection of the original species-as-classes concept. We have all learned, correctly, that Lamarck got it wrong. Organisms do not evolve – species do. But this idea often worded that *individuals* do not evolve, creating a language barrier that contributes greatly to the difficulty of grasping the reality of species.

So for Burma organisms may be real, but species are not. Yet in spite of the ontological difficulties posed by species concepts, Burma (1949, 1959) was quite willing to use the term "species" when identifying members of soil horizons, giving them a legitimacy beyond mere abstractions. In fact, in his seven-page paper on the genus *Theocampe*, Burma (1959) uses the term 102 times! I think he was quite comfortable with the idea of species as taxa despite his feigned distress with the ontology of species in his debate with Mayr. This is typical of most who engage in the species debate. We are all comfortable with the practical reality of species as real entities, but we are much less so when asked to define the species category conceptually.

Mayr's attempts to keep a lid on the species concept have been entertainingly futile (e.g. Mayr 1942, 1949b, 1982, 1996, 1997, 2000). Although his arguments were essentially correct, there were too many aspects of species that contained uncertainties (if not peculiarities) for the problem to go away. Refinement and thorough explanations of the BSC failed to arrest the problem, so it continued to expand.

In his response to Burma, Mayr (1949b) suggested paleontologists have no difficulty with the BSC, since they view soil horizons as moments in time. Their difficulty, according to Mayr, was with the meagerness of the fossil record. Burma, in his 1949 postscriptum to Mayr, suggested that, to the contrary, paleontologists do not agree uniformly on a species concept or even the objective reality of species. He felt that as the fossil record was enlarging, the gaps between species were subsequently shrinking. Therefore, if one could obtain a complete fossil record, the gaps would be eliminated altogether. Mayr's argument regarding paleontologists was prescient. The one paleontologist he did cite in his exchange with Burma was George Gaylord Simpson, who would soon challenge Mayr's species concept with his own evolutionary species concept (ESC). Their debate continued for decades.

By 1951, Simpson was developing the ESC, and the concept of typological species was all but gone, with the only members still promoting it to be fringe believers in saltation (Simpson 1951). Simpson's view of the ESC as "a lineage ... evolving independently of others, with its own separate and unitary evolutionary role and tendencies" recognized species as units of evolution. He even felt that a "unitary evolutionary role" would include asexual species. Simpson was looking for an overarching definition that would avoid competition with other species concepts, and he

accurately assessed the BSC as a method of determining whether the ESC had been achieved. He argued that geographical separation, morphological variation, reproductive barriers, and sympatry without introgression all provided evidence that the expectations of the ESC were being met. But he felt the criterion of reproductive isolation was an unnecessary requirement given that many species have achieved the necessary separation to evolve independently.

Mayr, not surprisingly, challenged Simpson's ESC. Regarding what Simpson termed as the "tendencies" of a species, Mayr (1997) asked how a population in nature could be classified by its fate in the future. These two influential biologists initiated an acceleration in the debates about species concepts that has only continued to ramp up.

Species nominalists such as Burma (who viewed species as real in name only) were the exception, even in the 1950s (Gregg 1950; Burma 1954). If we agree that species are real entities, as do most evolutionary biologists, rather than useful but arbitrary abstractions as viewed by species nominalists, a conceptual definition will or will not be accurate. Definitions that include some real species taxa but exclude others fail to provide an adequate overall definition of the species category – a common limitation of operational concepts.

A score or more of species concepts have been developed, but most are operational concepts that do not capture all the species and asexual entities that represent the length and breadth of biodiversity. Yet the value of most of these concepts is undeniable, because it is through a diversity of approaches that species taxa are identified. What is clear is that valid operational concepts are consistent with the overarching concept discussed earlier. In this way, these secondary concepts are not

components of a pluralistic approach to species, but are instead tools for diagnosing the monistic reality of biological species. Rather than competing definitions contributing to an imaginary species problem, they are compatible concepts consistent with an ontological understanding of species that has been in effect for decades.

Classes versus individuals

Some have appeared to support the contention that all taxonomic groups, as phylogenetic lineages, are qualitatively the same (Burma 1949; Baum 1998; Mishler 1999). But species taxa are unique among the taxonomic groups in that they are real entities that participate in real processes. The taxonomic species category is a *class* whose membership includes all the species taxa, from *Thermus aquaticus* to *Balaenoptera musculus*. So when people talk of species as a class (as in "We are going to learn about phyla today, and species tomorrow") they are referring to the species category. Each member of the species category is an instance of that class. Thus, a species member is a species, just like a phylum member is a phylum.

Getting confused yet? You should be! Let me rephrase the ideas in the last sentence of the previous paragraph. A member of the species category is a particular species taxon, just as a member of the phylum category is a specific phylum. (The fact that the term species is rarely qualified in this way contributes greatly to the presumption that there is a species problem.) Thus the species *Balaenoptera musculus* (the blue whales) is a member of the species category, and the phylum Chordata is a member of the phylum category. Both the phylum Chordata and the species *Balaenoptera musculus* might be described as individuals, since they are each, as lineages, unique things, but the

phylum Chordata is an individual only historically, named and defined in hindsight. Although the phylum Chordata is arguably monophyletic (Bourlat et al. 2006), its status as a phylum is an artificial construct mapped onto its hypothetical nodal position used for organizational purposes, with no clearly definable relationship to other phyla other than being a pigeon hole for lower taxonomic groups based on a useful but arbitrarily drawn line. That drawn line is a set of characters (including, in this case, a notochord or vertebral column) that define the members of the specific phylum, which are instances of that class.

Because the phylum Chordata is a class, it is composed of members. Each member shares the definition of the Chordata class, just as each nation is a member of the class of nations. One cannot point to the class of nations, since it is an artificial construct and has no location. But each nation (i.e. each member) shares the definition of that class. Furthermore, suprageneric biological taxa are all composed of members that are also classes, making them classes of classes. The phylum Chordata includes the class Mammalia, which in turn includes the orders Rodentia and Primata (among others). Each of these supraspecific taxa is a class, based on definitions, with members that meet the definition of their class. But most biologists agree that none of those supraspecific categories are real entities (Mayden 2002).

Species taxa, on the other hand, are unique among the taxonomic groups in a number of ways. First, species taxa are not composed of members that are instances of the taxon. Each species taxon is a real individual, not a class. You, as an organism, are a part of the species *Homo sapiens*. But you are not an instance; you are a component, not a member. *You are not a species – you are a part of one*. As such, species taxa cannot

be defined, but their component organisms can be identified as parts of a species taxon. Second, species taxa are real entities with spatial cohesion, however loose and widespread their component organisms may be. Third, species taxa participate in a process – the process of evolution. They do so as reproductive communities. In this way, they are real entities, and reproductivity is the mechanism of their coherence.

Although people typically think of an individual as a person (or perhaps an organism), the term is broader than that, referring ontologically to a distinct, cohesive, indivisible entity. Thus, many things qualify as individuals – like you, me, the planet Earth, the constellation Orion, the neighbor's orange tabby cat, the black-chinned hummingbird species, that particular black-chinned hummingbird currently drinking from a feeder with a few missing tail primaries (lost during a close encounter with the neighbor's orange tabby the previous day), and even one of those missing primaries spit out by the cat. Although our default idea of an individual is an organism, all but one of the examples listed above are easily intuited as individuals. The exception is a species taxon.

Many of us balk at the idea that a single species, which is typically composed of many individual organisms in one or more component populations, is itself an individual. It is not a viewpoint one grows up with, nor are species easily recognizable as individuals since we never see a species as a separate, cohesive unit (unless it is composed of a handful of organisms on the brink of extinction that can all be seen at once). At best we might see a herd of elk or a stand of trees, but we see neither in totality as a species. So we have not learned to recognize species as individuals or think of them as such. Yet all

species, like all of the previously mentioned examples of individuals, share a number of traits that identify them as individuals.

Although counterintuitive, the idea is not a new one. Ghiselin (1966) is credited with launching this viewpoint in the 1960s, and developing it further in the 1970s (Ghiselin 1974). It has since gained fairly wide acceptance (Stamos 2003). But there were earlier proponents, including Julian Huxley (1912), who pointed out nearly a century ago that "If evolution has taken place, then species are no more constant or permanent than individuals" and even described the "the species-individuality of which we are the parts."

By definition, any individual will come into existence and survive for a period of time before eventually ceasing to exist. In this way, each species is, like any clade, a unique historical entity. But unlike the higher clades (some of which are viewed as higher taxonomic ranks, such as order and class), species are also bounded spatially. Since higher clades are typically composed of numerous species, all having come into existence at different times and places, they cannot be bounded spatially. Such spatiotemporality contributes to the cohesion that is part and parcel of a species, contributing to its susceptibility, as a unit, to the process of evolution. The breaking of this spatiotemporality can lead to the divergence of a component population, beginning the speciation process.

Individuals are subject to, and participate in, processes. A species in nature is an individual that changes over time due to the process of evolution, and it constitutes the highest taxonomic group subject to this process. But once a species taxon has gone extinct, its spatiotemporality has been broken and it will not, and cannot by definition,

occur again – that is, species as individuals do not recur as instances, anymore than identical twins are occurrences of the same individual. Supraspecific clades are not real individual entities because they are not cohesive units that are involved in processes. They are merely abstractions based on historical monophyly – only recognized and identified in hindsight.

As unique individuals, species are given proper names. They (like you and I) are describable and identifiable, but not definable. Like the individual hummingbird at a feeder that had a full set of primaries the previous day, a species may not be the same from one moment to the next – yet as an individual it, in fact, exists and remains.

Species in nature have often been mistaken for classes whose members are the organisms that make up their populations. But rather than being members, those organisms are instead component parts, since no set of characters is both necessary and sufficient to describe all of the organisms that make up a species. No two parts (organisms) are definably alike (including clones) in a way that could characterize them as members of a class. None of the parts shares all the traits of the whole.

Like the single, disconnected hummingbird feather (an individual composed of a shaft and filaments, some of which are torn and broken), the list of individuals below the level of species is diverse – from individual populations of black-chinned hummingbirds to individual birds, feathers, filaments, filament molecules, and individual atoms. When speaking of any one of these things specifically, it cannot be defined – only described and pointed out – and none of these must remain the same, or even exist, from one moment to the next. Each is a single entity, bounded by time and place, with a beginning and an end, and participating in a process. Individuals below the species level (populations,

organisms, and parts of organisms) do not constitute the cohesive unit of evolution that defines the species category, and the taxonomic groups above (family, order, class, etc.) do not participate in the evolutionary process at all.

Why are there competing species concepts?

The proliferation of species concepts that has arisen since Mayr's Biological Species Concept in 1940, and particularly after Hennig's phylogenetics gained broad popularity, is in part due to specialists in various biological disciplines whose research involves species. For some, it is the types of species they study that biases their view of an ideal species concept, while for others it is the technologies with which they have expertise. Perhaps for some there is even the drive for personal recognition.

The proliferation of concepts (now over twenty, and surely to grow), and the fervor with which their proponents attempt to establish each as the ideal species concept, have become part and parcel of the species problem. Yet this component of the problem is a canard that has received undeserved attention. Many of these species concepts can and should in fact coexist, without presenting a case for pluralism. Since many do have validity and value as tools for detecting biodiversity, they deserve impassioned support, but not to the exclusion of others. Rather than being exclusive, with any one concept negating or superseding the others, most are instead methodological concepts suggesting a particular approach to species diagnosis.

As there are numerous roads to Rome, each legitimate operational species concept can help identify species. But each also has its limitations. Depending on the organism studied or the technology employed, one species concept may be better suited than

another for diagnosing particular species taxa. There may well be overlap in the species that are identifiable with two or more species concepts, but none of the operational concepts will identify all species taxa or every organism within a species. Thus, a general, overarching species concept needs to be recognized, one that subsumes the various valid operational concepts. Viewed in this light, the growing numbers of operational species concepts provide the tools for diagnosing species that adhere to the overarching species concept without contributing to the mythological species problem.

Mayden (1999) suggested just such a system, which he framed in a hierarchical construct. Recognizing the absurdity of the operational definitions dueling for recognition as the ideal species concept, he proposed a hierarchy of consilient operational concepts, under the umbrella of what he considers the only non-operational species concept that meets the goal of an overarching definition that will encompass the functionally operational concepts currently available. His primary species concept is a modification of Simpson's evolutionary species concept and Hennig's species concept. It provides an overarching concept that is non-operational, recognizes species as individuals, and is not biased by the types of taxa examined or the technologies used in identification. The operational concepts consistent with this overarching concept are subsumed under it, and provide multiple approaches to species identification. These operational concepts are thus secondary but necessary tools to recognize the full breadth of species biodiversity.

Textbooks continue the myth rather than offer ontological clarity

In many general biology and evolution textbooks, the species concept is presented in the later chapters, almost as if to avoid the issue. Freeman and Herron (2007) do not address species concepts until chapter 16 of their 20-chapter textbook. They state that, while all human cultures name and categorize organisms based on degrees of apparent similarity, biologists attempt to define species in a way that is "mechanistic and testable." Right away you see the need for a clarification of the term "species" from their failure to provide one. Are the authors talking about individual taxa, the species concept, an operational method of species identification, or something else? This ambiguity creates confusion on the issue, inflating the problem unnecessarily. The authors then define "a species" as "the smallest evolutionarily independent unit" and proclaim (without references) that this definition is the one "most biologists agree on." I, for one, find their definition vague to say the least, and probably incorrect. I would argue that a species taxon is not the smallest, but the largest evolutionarily independent unit (but the terms in such a statement would still need to be defined). The authors do say that each species has its own evolutionary trajectory, and that the spread of alleles stays within the populations of a species. Later in the chapter they also discuss aspects of speciation that are useful and informative. But the damage has already been done.

Following their errant definition, Freeman and Herron then describe three "species concepts" which they feel are the most important currently in use. They offer these examples to demonstrate the difficulty of establishing an effective species concept that can identify populations that are evolving independently. The fact that they describe these concepts as methods of species identification demonstrates their operational nature

rather than their use as primary concepts. The suggestion is that there are competing species concepts rather than numerous operational methods to identify species. They fail to sufficiently provide the ontological underpinnings to fully appreciate species concepts, and leave the reader with the suggestion of a continuing species problem.

Futuyma (2005) begins his discussion of species with the question, "What are species?" But the question is offered without context, and the reader is left to ponder whether it refers to specific taxa, individual organisms, encompassing concepts, or something else. The question is also raised late in the text, in chapter 15 out of 22. His introduction gives the impression that individual species can be defined, suggesting they are, therefore, classes based on character sets that identify members. Yet (like Freeman and Herron 2007) he offers no ontological discussion of classes versus individuals. He also pits a selection of operational species concepts against one another, apparently in competition for the conceptual holy grail, thus promoting the idea of a rancorous debate that is "as active now as ever before." The species problem is, in this way, passed on to students as a given.

In Barton et al.'s (2007) text Evolution, the subject is addressed in chapter 22 of 26 (I sense a pattern developing). Although they argue that species are real, they too fail to be clear about the concept they are discussing. After describing clinal variations in widely distributed populations and the challenges these can present, they begin the chapter in earnest with the heading, "There Are Several Ways of Defining Species." They begin by describing attempts to define individual taxa (which, as has been shown, cannot be defined). Finally, after demonstrating that sets of phenotypic characters fail at providing a definition, as do sets of molecular characters and even genealogies, their

solution is to shift the discussion away from attempts to define a taxon over to an examination of species concepts. This is unfortunate, since they had set the stage nicely to explain the ontological foundation of species taxa. Instead, their switch without explanation only adds mystery to the subject, and helps establish a sense of impenetrability to the species problem. Although the species concept they promote is the BSC (at least, for sexually reproducing organisms), they fail to provide a clear analysis as to why. With neither the ontological details of species taxa nor species concepts adequately addressed, this introductory chapter only assures confusion rather than shedding light on these critical subjects.

Strickberger (2000) tackles species concepts relatively early in chapter 11 of his 25-chapter textbook entitled "Evolution." But this section also begins with obscurity rather than clarity. "Among the variety of species definitions that have been offered, taxonomists have generally used morphological criteria, since this is how most individuals have been compared." By "species definitions" the author is referring to definitions of taxa. But if one could define a species, there would be more than just a "variety" – there would be as many definitions as there are species. Furthermore, he is suggesting that species taxa are definable by phenotypic character sets, which would make them, ontologically, classes. The subject of the species category is not even addressed, other than to refer to it as one of many taxonomic ranks.

All of these texts address important ideas regarding speciation and various methodologies for recognizing this process. They also provide interesting biological examples in their discussions on the subject of species identification and classification. But these otherwise intriguing chapters fail to provide the student with a clearly

constructed discussion of the most important concept in evolutionary biology. I am left to wonder if this omission is (1) intentional, in order to avoid a lengthy metaphysical discussion, or (2) a matter of textbook stubbornness, with old concepts and lessons failing to get updated, or (3) a failure by the authors to fully understand the various concepts themselves. Perhaps they simply presume that the species problem is a given, and are victims of the myth themselves, as so many of us are. Even if they are aware of the ontology of species concepts, and that individual taxa are undefinable but identifiable individuals, perhaps they find it simpler in an introductory text to offer a hint of evolutionary cohesion and a taste of various operational methods for identifying members of a cohesive and divergent population. In this way they provide their students a glimmer of understanding while injecting a sense of debate and opportunities for future research. This might encourage students to pursue answers to these apparently unresolved questions. Unfortunately, they also establish and promote the mythical problem to the next generation of potential biologists who might otherwise pursue questions that actually need answers.

One of the values of textbooks is to alert students to areas of uncertainty that need research, and hopefully stimulate some to pursue work in those areas. But in this case, uncertainty is introduced unnecessarily, and clarity that should be provided is not. The unnecessary confusion that results may well be a barrier to effective research and a threat to biodiversity due to the political consequences of the survival of the species problem. Species are real, but the species problem is a myth.

Recap and Conclusion

The first species concept to gain wide acceptance was an erroneous idea grounded in mysticism. Species were considered perfect templates created by God, eternal and unchanging, from which their constituent populations of organisms were created and replenished. A more accurate, secular view was developed by Ionian natural philosophers, but by dint of historical accident, it never gained sway. The erroneous, mystical view had more than a 2000-year run – originating with Pythagoras, modified and enshrined by Plato, maintained by Augustine, modernized by Aquinas, and given scientific substantiation by their natural-theologian offspring. During that great span of time, this concept had near unanimous acceptance, so there was no species problem. Given that long period of certainty, this errant view would not be easily abandoned.

A real species problem emerged when Darwin challenged the millennial belief in species stasis with his theory of gradual species change via evolution by natural selection. Darwin's theory of evolutionary speciation soon won out among scientists, but they fought amongst themselves over gradualism versus saltationism, and the debate only accelerated when Mendel's research came to light. As Darwin's theory solidified and matured with confirming evidence and new insights, the species problem paradoxically expanded with competing conceptual views, and this pattern has not abated.

The Modern Synthesis (Provine 1971) brought Mendelian heredity in line with population genetics, but it did not stem the tide of newly devised species concepts. By the 1960s, the methods of phylogenetics had been developed and species were recognized as individuals rather than classes. Debates regarding the best species concept were

becoming matters of detail, and the species problem was now one of perception and holding on to the past.

The final tumblers fell into place in the 1960s and 70s when a biological species in nature was recognized as a group of sexually reproductive organisms in one or more populations forming a cohesive unit – a separate lineage on its own evolutionary trajectory. Similar versions of this overarching definition had been given before, but species taxa had still been considered classes whose members could be recognized by defining characters. The millennial belief in species as classes may well have created a collective comfort with the notion of definable species. Now that species were recognized as unique individuals, indefinable but identifiable as such, the fully mature species concept was revealed.

Although the species problem had finally been solved, it remained difficult to appreciate and was not widely recognized. Debates over the ideal species concept not only continued, they gained momentum. Most of the popular competing concepts were operational methods for identifying organisms as members of one species or another. These valuable products of developing technologies and specialized disciplines fit neatly as tools of species identification under the overarching species concept. Yet the false impression of competition and incompatibility between these various operational concepts established the mythical species problem that has persisted to the present. When an operational species concept is presented as an overarching one, it is easily criticized for failing to identify all species, providing fuel for the debates. Remove the expectation of universality, and the concept is recognized as a useful tool for species identification rather than an exclusive species concept.

The species problem is historical, not extant – solved over 30 years ago. The myth of the species problem was born when the solution was provided, and it remains as a product of incomplete information and an unconscious attachment to the historical doctrine of species as classes. This mythical problem will be maintained as long as it continues to be propelled by unnecessary debates and promoted with errantly presented lessons in introductory texts. It is long past time to relegate this mythical problem to history.

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CHAPTER 3

THE TAXONOMIC DESIGNATION OF *ERIOGONUM CORYMBOSUM* VAR. *NILESII* (POLYGONACEAE) IS SUPPORTED BY AFLP AND cpDNA ANALYSES[1]

ABSTRACT

We examined populations of perennial, shrubby buckwheats in the *Eriogonum corymbosum* complex and related *Eriogonum* species in the subgenus *Eucycla*, to assess genetic affiliations of the recently named *E. corymbosum* var. *nilesii*. The known populations of this variety are all located in Clark County, Nevada, USA. We compared AFLP profiles and chloroplast DNA sequences of plants sampled from populations of *E. corymbosum* var. *nilesii* with those of plants representing other *E. corymbosum* varieties and related *Eriogonum* species from Colorado, Utah, northern Arizona, and northern New Mexico. We found evidence of genetic cohesion among the Clark County populations as well as their genetic divergence from populations of other *E. corymbosum* varieties and species. The genetic component uncovered in this study supports the morphological findings upon which the nomenclatural change was based, attesting to the taxonomic distinctness of this biological entity.

INTRODUCTION

The Polygonaceae comprises a large and diverse angiosperm family that includes 48 known genera with approximately 1,200 recognized species (Freeman and Reveal 2005). Several studies have demonstrated the monophyly of the family (Chase et al.

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1993; Cuenoud et al. 2002; Lamb-Frye and Kron 2003; Sanchez and Kron 2008) but sorting out taxonomic relationships within Polygonaceae has been a long-standing challenge. It has been suggested that the difficulties in determining relationships, particularly in the subfamily Eriogonoideae, may be due to relatively recent and rapid diversification (Welsh et al. 2003; Sanchez and Kron 2008).

Numerous subfamilial circumscriptions within the Polygonaceae have been based on morphological characters (e.g. Arnott 1832; Luerssen 1882; Roberty and Vautier 1964; Reveal 1978, 1989; Freeman and Reveal 2005). Molecular studies (Chase et al. 1993; Lledo et al. 1998; Cuenoud et al. 2002) failed to support the earlier classifications. More recently, Lamb-Frye and Kron (2003) analyzed Polygonaceae with chloroplast *rbcL* sequences and Sanchez and Kron (2008) included additional cpDNA sequences along with portions of the nuclear gene *LEAFY*. Findings of both studies supported monophyly of Polygonaceae and its subdivision into two redefined clades – Polygonoideae and Eriogonoideae.

Eriogonoideae sensu Sanchez and Kron (2008) include several species endemic to the southwestern United States (Welsh 1978; Meyer 1986; Archibald et al. 2001; Reveal 2004b). This area appears to comprise a zone of adaptive radiation, with endemics from other plant families found there as well (Meyer 1986; Nickrent and Wiens 1989; Sivinski and Knight 1996; Douglas and Manos 2007). The narrow ranges for some endemic taxa may point to recent diversification in this arid region of North America (Reveal 1989, 2005; Sanchez and Kron 2008). Edaphic factors, including gypsum-rich soils, may play a role in plant diversification and endemism in North America's southwestern deserts (Maschinski et al. 2004; Drohan et al. 2006; Douglas and Manos 2007; Moore and Jansen

2007). Glacial and post-glacial climate change may also have contributed to taxonomic divergence through range contraction and expansion, fragmentation, and hybridization of taxa (Comes and Kadereit 1998; Fehlberg and Ranker 2009). This putative history of recent divergence may explain past difficulties in determining relationships within the Eriogonoideae.

The *Eriogonum corymbosum* Benth. complex (Eriogonoideae), as currently recognized, comprises a group of buckwheat taxa distributed across the western U.S., from southwestern Wyoming, through Utah and southwestern Colorado, to northern Arizona, northern New Mexico, and southern Nevada (Reveal 2005). Across the range, these woody shrubs vary in size, leaf shape and surface structure, predominant flower color, and overall habit, among other aspects of morphology. A putative history of dispersion, isolation, divergence, hybridization, and introgression may have contributed to the group's morphological and geographical diversity (Reveal 2002; Welsh et al. 2003). This species complex has been revised on several occasions (e.g. Jones 1903; Reveal 1967, 2002, 2005), with eight varieties currently recognized.

Until recently, predominantly yellow-flowered populations of *E. corymbosum* in Clark County, Nevada, have been treated either as the wide ranging *E. corymbosum* var. *glutinosum* (Reveal 2002) or the more narrowly distributed *E. corymbosum* var. *aureum* (Reveal 1983, 1985). Identification of *E. corymbosum* var. *glutinosum* had previously hinged primarily on flower color (with predominantly yellow-flowered plants identified as variety *glutinosum*). However, Reveal (2002) pointed out that flower color in the predominantly yellow-flowered *Eriogonum* Michx. taxa can vary among individuals within populations, which often include white or cream-colored members. In our field

observations we also found this to be the case. Although yellow flower color is a useful, in combination with other traits, for identifying subspecific taxa within *Eriogonum*, flower color alone is not definitive for any variety.

The only known population of *E. corymbosum* var. *aureum* is located north of St. George, Utah (Appendix A; Figs. 3.1, 3.2), a predominantly yellow-flowered variety distinguishable from variety *glutinosum* based on glabrous branches of the inflorescence (Reveal 2005). This trait also separates variety *aureum* from the predominantly yellow-flowered plants in the *E. corymbosum* populations of Clark County, Nevada, whose flowering branches tend to be silvery-pubescent. Both sides of the leaves of the Clark County plants are silvery-pubescent, separating them from varieties *glutinosum* and *aureum*. Based on these traits, as well as ecological considerations, Reveal (2004a) concluded that the Clark County populations are morphologically and ecologically distinct and geographically disjunct from both *E. corymbosum* varieties *glutinosum* and *aureum*, and he proposed the new varietal designation *nilesii* (Niles's wild buckwheat). The known populations of *E. corymbosum* var. *nilesii* are mainly in and around Las Vegas and the Muddy Mountains region of Clark County, Nevada (Reveal 2005).

Concerns have been expressed regarding the loss of the Clark County populations of *E. corymbosum* var. *nilesii* as a result of development and off-road vehicle recreation, and questions about its taxonomic status have been raised (Reveal 2004a). *Eriogonum corymbosum* var. *nilesii* is currently listed by the Bureau of Land Management (BLM) as a sensitive species (Boettinger et al. 2007) and the U.S. Fish and Wildlife Service (USFWS) recently selected it as a candidate for protection under the Endangered Species Act of 1973 (ESA) (USFWS 1983; Perkins and Samargo 2008). Further evidence

demonstrating the taxonomic distinctness of *E. corymbosum* var. *nilesii* would lend support to an ESA listing, whereas evidence to the contrary might suggest that the Clark County populations are part of a more widespread taxon.

Here we examine populations in the *E. corymbosum* complex and related *Eriogonum* species in the subgenus *Eucycla* to address the genetic distinctness of the populations of *E. corymbosum* var. *nilesii* found in Clark County, Nevada. By analyzing a combination of amplified fragment length polymorphism (AFLP) and chloroplast DNA (cpDNA) data, we evaluate the conclusion of Reveal (2004a) that the Clark County populations of *E. corymbosum* have diverged in a manner and to an extent that warrants this varietal recognition.

MATERIALS AND METHODS

Collections

Based on recorded locations from herbarium specimens and personal communications with numerous field biologists, we surveyed for *Eriogonum corymbosum* and related *Eriogonum* taxa from southern Nevada, northern Arizona, and northern New Mexico north through Utah and into Colorado. We collected leaf samples of 10-15 plants from each of 51 populations representing 12 *Eriogonum* species within the subgenus *Eucycla* (Appendix A and Table 3.1; Figs. 3.1, 3.2). Each collection site, referred to as a population, comprises a geographically bounded and relatively isolated group of potentially interbreeding individuals.

Leaf samples were dried rapidly on silica gel inside sealed plastic bags. Sampled populations included individuals from six varieties of *E. corymbosum*. We sampled 10

populations that we identified morphologically as *E. corymbosum* var. *nilesii* (Fig. 3.2), nine of which were located in and around Las Vegas, Nevada. Samples of the tenth population (N10) were collected from White Basin in the Muddy Mountains region about 40 km east of North Las Vegas. These 10 sites were all located in Clark County (referred to as variety *nilesii*). Additionally, samples from an eleventh Nevada population (referred to as N11) that appeared phenotypically most similar to variety *nilesii* were collected in Lincoln County about 15 km west of Utah's southwest corner and 100 km northeast of the Las Vegas plants (Fig. 3.2). Although there is only one confirmed population of variety *aureum* (which we sampled), we located and sampled three additional populations that keyed most closely to variety *aureum*, and in this paper we refer to them as such.

A protocol was followed at each collection site to avoid bias in the sample-selection process. After surveying to determine the general boundaries of a population, a central transect was marked through the length of the population. Plants were sampled by walking the transect and selecting consecutive plants near the transect that were at least 5 m apart (in order to avoid selecting clones). If too few plants were sampled following this method, plants were sampled further from the transect, while again ensuring they were at least 5 m from any other sampled plant. Ten to 15 leaves were collected per plant (more for taxa with very small leaves). Individual plants were sampled if they had enough healthy leaves (60 or more) to ensure that sampling would not be likely to cause lasting damage to the plant. Plants were not, however, selected based on size, apparent age, or other morphological features. Plant vouchers for each collection site are deposited at Utah State University's Intermountain Herbarium (UTC).

DNA extraction

Genomic DNA was extracted from the dried leaf samples using the Qiagen DNeasy 96 Plant Kit and the Qiagen DNeasy Plant Mini Kit (Qiagen, Inc., Valencia, California) following the instructions of the manufacturer. Concentrations of DNA in the extracted sample solutions were quantified with the NanoDrop ND-1000 spectrophotometer (Nanodrop Technologies, Wilmington, Delaware). Extracted DNA solutions were stored at –80°C until use.

Amplified Fragment Length Polymorphisms

An AFLP profile was generated for each DNA sample using a modified version of the protocol by Vos et al. (1995). The extracted DNA was digested with restriction enzymes (with the rare cutter *Eco*RI and the frequent cutter *Mse*I) then ligated with forward and reverse adaptors. A subset of the fragments was amplified by polymerase chain reaction (PCR) using an *Eco*RI/*Mse*I primer pair set, with an additional selective nucleotide on each primer: *Eco*RI+A and *Mse*I+A. This +1 PCR reaction was followed by a +3 PCR reaction in which 2 additional selective nucleotides were added to the primer pair sets. We used two different +3 primer pair combinations with the +1 PCR product: *Eco*RI-ACG with *Mse*I-ACT and *Eco*RI-ACC with *Mse*I-AGC. The amplified restriction fragments were separated via capillary electrophoresis and recorded using Applied Biosystem's ABI 3730 DNA Analyzer with LIZ-500 size standards. The AFLP profile generated from each DNA sample was visualized and scored using Genographer v1.6.0 (Benham 2001). We replicated 32 (8.2%) of the samples to determine the error rate in band scoring.

The AFLP technique amplifies regions of the genome randomly and many polymorphisms can be found, representing variation among individuals via presence or absence of restriction sites and the selective nucleotides. From the scored fragments generated by the +3 primer pair sets, we selected 103 polymorphic loci based on data quality and bimodality of signal across the dataset, varying in size from 66-476 bp, and obtained AFLP profiles from an average of 8 plants per population (on which we based our analyses).

We examined the AFLP data with Principal Components Analysis (PCA) using the program NTSYSpc v. 2.10t (Rohlf 2000). This multivariate analysis constructs a set of three orthogonal coordinate axes from the first three eigenvalues (derived from the presence/absence data) and projects the individual samples as points in a scatter plot within these three axes such that variance is maximized in as few dimensions as possible. Representing the variance extracted by each axis, eigenvalues can be summed as a percentage of the total variance. This exploratory approach rapidly provides graphical 3-D correlation matrices that demonstrate potential clustering.

For further insight into the data, we analyzed the AFLP sample profiles using a model-based method. The program Structure 2.2 utilizes a Bayesian approach to infer related clusters (*K*) of individuals from multilocus genotype data while also evaluating the strength of evidence for the inferred clusters (Pritchard et al. 2000, 2007; Falush et al. 2007). Structure starts with an arbitrary parameter configuration that iteratively updates via a Markov Chain Monte Carlo (MCMC) algorithm until converging on the posterior distribution of all the parameters based on the data available (Pritchard et al. 2000). Each individual is assigned to a cluster according to its genetic makeup, represented by a

vector *q*, which gives the percentages of that genetic makeup (if any) originating from each of the populations recognized by Structure. Although Structure was developed for diploid genotypic data that provide allelic information, Falush et al. (2007) extended the MCMC algorithm to account for the partial information provided by dominant markers (such as AFLPs).

We analyzed sampled populations of *E. corymbosum* var. *nilesii*, *E. corymbosum* var. *aureum*, *E. thompsoniae*, and population N11 with Structure set to the admixture model. We tested for the number of genetic clusters by running five replicates for each of six simulations, from $K = 1$ to $K = 6$, with 100,000 MCMC iterations after a burn-in of 30,000 (following Pritchard et al. 2000 and Pritchard et al. 2007).

Chloroplast sequencing and phylogenetic analysis

We amplified and sequenced the *trnS*^{UGA}-*trnfM*^{CAU} cpDNA intergenic spacer region for 54 individuals from 13 different *Eriogonum* taxa using primers described by Shaw et al. (2005). We designed a third internal primer to ensure base clarity throughout the length of the cpDNA sequences. We amplified this region using PCRs in 50µL solutions and purified the PCR products using Qiagen's Qiaquick Purification Kits (Qiagen, Inc.). Sequencing reactions of the purified PCR products were run in both directions in separate reactions for each sample with each primer and Amersham's ET Dye Terminator.

The products of the sequencing reactions were purified through hydrated Sephadex and then run on the ABI 3100 automated capillary sequencer (Applied Biosystems). Contigs were assembled and sequences confirmed using Sequencher

v.3.1.1 (Gene Codes, Ann Arbor, Michigan). The initial alignment for all sequences was obtained with the Clustal-W Multiple Alignment option in the BioEdit alignment program (Hall 1999). The final alignment was obtained manually, creating a trimmed sequence matrix with 1,222 characters. Nucleotide sequences are deposited in GenBank as accession numbers FJ204255 through FJ204308.

The aligned sequences were imported into PAUP v4.0b10 (Swofford 2002) and analyzed under the parsimony optimality criterion. All characters were analyzed as equal in weight and unordered, with gaps treated as missing. Tree space was examined with a heuristic search with simple addition sequence, the tree-bisection-reconnection (TBR) branch-swapping algorithm, and the MulTrees option in effect, keeping all trees. We used *E. effusum* samples to root the tree. Additionally, bootstrap values were calculated for 1000 replicates and plotted onto the parsimony tree to evaluate relative branch support (Felsenstein 1985). The dataset for this phylogenetic analysis was submitted to TreeBASE (study accession number S2268, matrix accession number M4317).

RESULTS

AFLP reproducibility

Before running analyses on the AFLP matrix, we examined the similarity of the 32 AFLP replicates to assess the reproducibility of the data. The results from the replicated samples showed a locus-scoring error rate of 1.09% over 103 loci within the AFLP data matrix. This error rate is relatively low for AFLP studies (when rates are reported) and it should not bias our analytical results.

AFLPs: Principal Components Analyses

PCA 3-D graphs derived from the AFLP data matrix demonstrate genetic similarities among populations. The graphical distances of *E. effusum* and *E. racemosum* from the other taxa tested are apparent in Fig. 3.3. With those two taxa removed from the data matrix, a PCA shows two large clusters (Fig. 3.4). One of these two main clusters is a broadly connected group composed of three subclusters: a subcluster of *E. corymbosum* var. *nilesii* samples at one end, a more loosely associated subcluster of *E. thompsoniae* samples at the other, and spread between these two subclusters are all the sampled individuals identified as *E. corymbosum* var. *aureum* as well as the Nevada population N11 from Lincoln County. Three individuals identified as *E. corymbosum* var. *glutinosum* are also part of this large cluster, most closely associated with the *E. corymbosum* var. *nilesii* subcluster. The second large cluster includes all other varieties of *E. corymbosum* (including 16 samples of *E. corymbosum* var. *glutinosum* from 2 populations) along with the remaining *Eriogonum* species.

To bring further clarity to the main cluster containing *E. thompsoniae* and *E. corymbosum* var. *nilesii* and var. *aureum*, we ran another PCA with those individuals only, excluding the three members of *E. corymbosum* var. *glutinosum* (which will be examined more closely in another PCA). In Fig. 3.5, the samples of variety *nilesii* from the vicinity of Las Vegas (from populations N1-N9) and White Basin (population N10) can be seen as a tightly packed and separate cluster. The adjacent cluster, formed by members of variety *aureum* and the Lincoln County plants (N11), bridges the gap between variety *nilesii* and *E. thompsoniae* with some overlap between a few samples from populations of *E. thompsoniae* and *E. corymbosum* var. *aureum*. The first three

principal components captured 44.1, 8.6, and 3.3% of the variance in the data set respectively.

Although there were too few samples of *E. corymbosum* var. *glutinosum* from U8 to draw any conclusions with confidence, we examined the graphical relationship between the three samples from U8 and the samples of *E. corymbosum* var. *nilesii* from populations N1-N10 in a separate PCA (Fig. 3.6). The samples of variety *glutinosum* were peripheral to the cluster of variety *nilesii* samples.

AFLPs: Structure 2.2 analyses

Using the program Structure 2.2 (Pritchard et al. 2007), we analyzed the AFLP profiles of all individuals sampled from populations designated as *E. thompsoniae*, *E. corymbosum* var. *aureum*, *E. corymbosum* var. *nilesii*, and those from population N11. In our tests to determine *K*, with each increasingly larger simulation the probability of *K* was higher, but even at $K = 6$ it was vanishingly small (at $2.045*10^{-6}$). We attributed this to the putative complexity of the populations in the St. George region of Washington County, Utah and population N11 in adjacent Lincoln County, Nevada. Such results are not infrequent when data sets are not all genetically discrete populations, and in such cases it is recommended to choose a biologically reasonable value for *K* that also appears to capture most of the structure (Pritchard et al. 2000, 2007; Falush et al. 2007). We therefore selected $K = 3$ as a realistic estimation, given that three taxa were presumed to be involved. As with the PCA analyses, no population information was given for any of the individual AFLP profiles. Structure assigned each individual probabilistically to one

of three clusters, but a number of apparently admixed individuals had affiliations with more than one cluster.

With the Structure output arranged with the individuals in order by presumed taxon (Fig. 3.7), the cluster of all individuals from the Clark County populations of *E. corymbosum* var. *nilesii* showed very little evidence of admixture from the other two groups. However, many of the individuals in the second group (composed of all the *E. corymbosum* var. *aureum* samples and the samples from population N11) showed admixture from both of the other two clusters. The third cluster, composed of samples identified as *E. thompsoniae*, included some that showed admixture as well – especially from members of *E. corymbosum* var. *aureum* populations.

Chloroplast sequence analyses

Among the 13 taxa and 54 individuals we successfully sequenced, there were 17 different haplotypes due to 24 substitutions and 10 indels. Of the 24 variable characters in the PAUP parsimony analysis, 21 were parsimony-informative.

The analysis found a single most parsimonious tree (Fig. 3.8). All Clark County, Nevada samples of *E. corymbosum* var. *nilesii* had identical sequences, and shared their haplotype with individuals from two populations of *E. corymbosum* var. *aureum* (U35 and U36) and one population of *E. thompsoniae* (U32). The haplotype most similar, but not identical, to that of the Clark County, Nevada samples of *E. corymbosum* var. *nilesii* was shared by the two samples from population N11 (Lincoln County, Nevada), an *E. corymbosum* var. *glutinosum* sample from U08, and members of two other populations of *E. thompsoniae* (U19 and U33).

DISCUSSION

The populations of *E. corymbosum* in Clark County, Nevada, have been grouped at different times in the past with two established varieties – either variety *glutinosum* or variety *aureum* – based on habit and flower color, among other phenotypic traits (Reveal 1967, 1985, 2002). Recently, Reveal (2004a) argued that the Clark County populations were morphologically and ecologically distinct enough to warrant a new taxonomic designation, which he named variety *nilesii*. Our comparison of the Clark County populations, using AFLP markers and cpDNA sequence data, supports Reveal's conclusions. We found demonstrable genetic cohesion among *E. corymbosum* individuals sampled from populations in Clark County, Nevada. Not only did the sampled individuals form a tight group isolated from sampled populations of other *E. corymbosum* varieties and related species in both PCA and Structure analyses, the Structure analysis also demonstrated that they are independent from their most closely related taxa (demonstrating little or no evidence of introgression).

Eriogonum corymbosum var. *aureum*, the taxon which we attributed to a number of populations in and around St. George, Utah, appears to be the closest relative of *E. corymbosum* var. *nilesii*. We also found an apparent relationship between the predominantly herbaceous species *E. thompsoniae* and *E. corymbosum* var. *nilesii*, linked by their mutual relationships to *E. corymbosum* var. *aureum*. Although a geographically distant and morphologically distinct population of *E. corymbosum* var. *glutinosum* with only three individuals tested (U8 in Appendix A) needs further examination, all other

Eriogonum varieties and species that we tested (including two other populations of variety *glutinosum*) were members of more distantly related clusters in our analyses.

The relationships of *E. corymbosum* var. *nilesii* to variety *aureum* and *E. thompsoniae* are demonstrable in our AFLP and sequence results. Although variety *nilesii* forms a tight and separate cluster in our PCA analyses (Figs. 3.4-3.6) and Structure analysis (Fig. 3.7), the association of this taxon with the loosely formed cluster that includes variety *aureum* and *E. thompsoniae* may be the result of its past migration and hybridization with *Eriogonum* taxa in Utah. Given that the Structure and NTSYS programs employ different algorithms to group the genetic profiles of samples, the similar clustering arrangements they provided add corroborative support to our conclusions. The sequence analysis adds additional evidence that *E. corymbosum* var. *nilesii* is a distinct taxon whose nearest relative is variety *aureum*. These results indicate that variety *aureum* may be a hybrid and repository of genes from both variety *nilesii* and *E. thompsoniae*, thereby providing a conduit for introgression between them. In that regard, the Structure analysis shows introgression by attributes characteristic of *E. corymbosoum* var. *nilesii* into both *E. corymbosum* var. *aureum* and *E. thompsoniae*, but no obvious evidence of the reverse (Fig. 3.7).

While PCA analyses show a clear genetic separation of *E. corymbosum* var. *nilesii* and *E. thompsoniae* (Figs. 3.4, 3.5), the Structure analysis suggests that a number of *E. thompsoniae* individuals share genetic characters with *E. nilesii* (Fig. 3.7). Interestingly, the *E. thompsoniae* population that appears in our AFLP tests to be least influenced by *E. corymbosum* var. *nilesii* or var. *aureum* (U32; Fig. 3.7) shares the cpDNA haplotype common to all the Clark County samples of variety *nilesii* (Fig. 3.8),

echoing the Structure findings. So even this distinctive *E. thompsoniae* population may have a historical relationship with *E. corymbosum* var. *nilesii*.

The loose relationships between the samples of *E. corymbosum* var. *aureum* and *E. thompsoniae* – the broad spread of their genetic variability and the degree of overlap between the two taxa as demonstrated in Figure 3.5 – suggest continuing migration and hybridization. The region of southern Utah bordering southern Nevada and northern Arizona, where *E. thompsoniae* and *E. corymbosum* var. *aureum* populations are found, appears to be a zone of hybridization between these two taxa, and contributions to these populations from *E. corymbosum* var. *nilesii* may explain the patterns we found in our analyses. Perhaps not coincidentally, this region is also a transition zone between the Mojave desert (which encompasses Clark County's populations of variety *nilesii*) and the southwestern portion of the Colorado Plateau (the region where variety *aureum* and *E. thompsoniae* reside). Population N11 apparently lies on a contact zone between taxa from the two regions.

In contrast, the relatively cohesive nature of Clark County's *E. corymbosum* var. *nilesii* samples (Figs. 3.5, 3.6) suggests little influence on those populations by either *E. corymbosum* var. *aureum* or *E. thompsoniae*. This distinctness is also apparent in the Structure analysis, with little or no evidence of introgression from either *E. corymbosum* var. *aureum* or *E. thompsoniae* apparent in the Clark County samples (Fig. 3.7). Thus, the patterns we found may be the result of the long establishment of *E. corymbosum* var. *nilesii* as a distinct taxon while genetic exchange between populations of *E. corymbosum* var. *aureum* and *E. thompsoniae* appears to be ongoing.

Taxonomic designation

The species taxon, as the fundamental unit of evolution, is unique among taxonomic ranks, designating a population or a cohesive group of populations composed of sexually reproductive organisms forming a separate lineage on its own evolutionary trajectory (Zimmerman 1959; Simpson 1961; Hennig 1966; Mayr 2000; Wiley and Mayden 2000; Ghiselin 2002; de Queiroz 2005; Rieseberg et al. 2006). The infraspecific taxonomic rank designated as variety, on the other hand, denotes a population or group of populations presumed to have the potential to eventually gain the necessary separation to achieve their own evolutionary path. But where does one draw the line? Charles Darwin's (1875) view of varieties as "incipient species" remains conceptually accepted today, but he provided no methodology of discerning such taxa. O'Brien and Mayr (1991) suggested that populations could be recognized as subspecies if 1) their members can be identified by phylogenetically concordant phenotypic traits, 2) they are found in a unique habitat or geographic range, and 3) they demonstrate a unique natural history compared to any other subdivisions within the species. The apparently disjunct set of Clark County populations of *E. corymbosum* var. *nilesii* meets these requirements. But phenotypic traits might not be genetically based (Haig et al. 2006), particularly in plants (which can show edaphic and other environmental effects phenotypically), and the geographic separation might merely demonstrate distance but not divergence. More is required than a phenotypically diagnosable population or set of populations within a defined geographic range and habitat in order to demonstrate potential evolutionary independence.

The *seventy-five percent rule* provides a quantitative, although arbitrary, method whereby 75% of the members of the population of interest must be separable from all members that make up the overlapping population (Amadon 1949; Patten and Unitt 2002). This method also suffers from the subjective approach to choosing characters used to determine any overlap. Still, although some members of the Clark County populations of *E. corymbosum* var. *nilesii* show a close relationship to *E. corymbosum* var. *aureum* in all our AFLP-based analyses, there is no overlap. If we identify the population N11 as part of *E. corymbosum* var. *nilesii* (based only on morphological similarity) then the proportion of members separable in our AFLP tests becomes 88%, and the criterion is also met.

A more effective approach to assigning infraspecific designations to populations of sexually reproductive organisms is to demonstrate multiple lines of mutually corroborative evidence that demonstrate the populations as distinctive entities evolutionarily (Haig et al. 2006). We have shown here the genetic cohesion between *E. corymbosum* var. *nilesii* samples and their divergence from all other closely related taxa tested, using AFLP and cpDNA markers. Our results corroborate Reveal's (2005) description of *E. corymbosum* var. *nilesii*'s unique geographic range, habitat, and morphological distinctiveness in relation to other varieties. Some of the phenotypic characters Reveal examined, such as leaves that are "white-lanate to densely white-tomentose abaxially, silvery-floccose adaxially," also suggest the adaptive divergence of *E. corymbosum* var. *nilesii*, making it particularly well suited to the harsh desert climate of the Mojave. And the suggestion that *E. corymbosum* var. *nilesii* may be an edaphic "extremophile" (Drohan et al. 2006) adds further support to its adaptive divergence.

Given these multiple lines of evidence for the cohesion of Nevada's Clark County populations and their evolutionary divergence from other populations of *E. corymbosum*, the description of the set of Clark County populations as variety *nilesii* is strongly supported.

One might argue, given the confluence of evidence for genetic cohesion between the subpopulations in Clark County and their evolutionary divergence from other taxa, that *E. corymbosum* var. *nilesii* populations form a cohesive unit that deserves recognition as a species rather than a variety. Its apparent allopatry, possible edaphic endemism, and ecological value to the Mojave ecosystem all suggest its existence as a separate taxonomic entity on its own evolutionary trajectory. But its close genetic association to *E. corymbosum* var. *aureum* and one population of var. *glutinosum*, and its morphological similarity to the N11 population, provide a gray area that requires further study with wider sampling before one might conclude that Nevada's Clark County populations constitute a unique species of buckwheat.

Future work

The similarity found between *E. corymbosum* var. *nilesii* and one population of *E. corymbosum* var. *glutinosum* should be examined more closely. It is possible that *E. corymbosum* var. *aureum* is the result of hybridization between *E. corymbosum* var. *nilesii* migrants and *E. thompsoniae*, and that *E. corymbosum* var. *nilesii* is a long-established lineage that may have diverged from a variety like *E. corymbosum* var. *glutinosum*.

It has been suggested that *E. corymbosum* var. *nilesii* is an edaphic "extremophile" that may have established a niche in the soils derived from a Pleistocene marsh environment and now found in arid Mojave regions of Clark County, Nevada (Drohan et al. 2006). Perhaps soil endemism provides the isolation to protect this distinctive variety of *E. corymbosum* from introgression by other taxa, maintaining the stability and cohesion of its populations. Further work to verify the edaphic regime of *E. corymbosum* var. *nilesii* would be worth pursuing.

An ecological study of *E. corymbosum* var. *nilesii*'s structural importance on the landscape would be a valuable contribution since it appears to be the dominant plant species in the places where it thrives. Its cover percentages relative to other plant taxa appears to be significant, its soil holding properties may be important, and its relationships with other organisms may be extensive. Finally, an examination of ploidy levels could provide a clearer picture of the relationships within the E. corymbosum complex, and provide a window into the history of hybridization within this group.

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TABLE 3.1. Seventeen *Eriogonum* taxa sampled from 51 populations. Identifications following Reveal (2005).

Taxon	Map Code & # of sites
Eriogonum corymbosum var. *aureum* (M. E. Jones) Reveal	Eca-4
Eriogonum corymbosum var. *corymbosum* Benth.	Ecc-5
Eriogonum corymbosum var. *glutinosum* M. E. Jones	Ecg-3
Eriogonum corymbosum var. *nilesii* Reveal	Ecn-10
Eriogonum corymbosum var. *orbiculatum* (S. Stokes) Reveal & Brotherson	Eco-5
Eriogonum corymbosum var. *velutinum* Reveal	Ecv-3
Eriogonum corymbosum (ambiguous)	N11-1
Eriogonum effusum Nutt.	Ee-2
Eriogonum brevicaule Nutt.	Eb-1
Eriogonum hylophylum (Reveal & Brotherson) S. L. Welsh	Eh-2
Eriogonum lancifolium Reveal & Brotherson	Ela-1
Eriogonum leptocladon Torr. & A. Gray	Ele-2
Eriogonum loganum A. Nelson	Elo-1
Eriogonum microthecum Nutt.	Em-2
Eriogonum nummulare M. E. Jones	En-1
Eriogonum racemosum Nutt.	Er-1
Eriogonum smithii Reveal	Es-2
Eriogonum thompsoniae S. Watson	Et-5

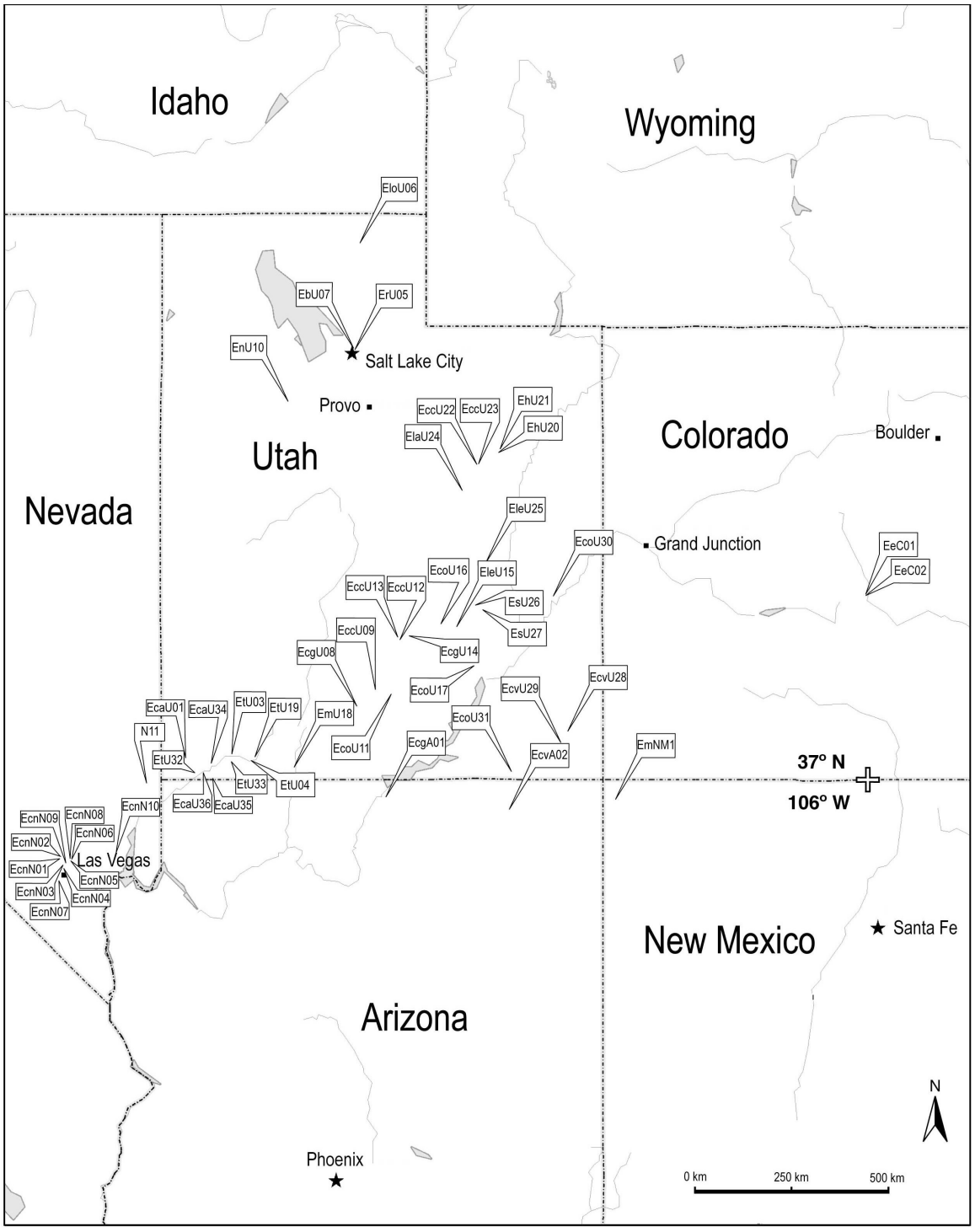

FIG. 3.1. Collection sites (11 in Nevada, two in Arizona, one in New Mexico, 35 in Utah). See Table 3.1 for key to abbreviations.

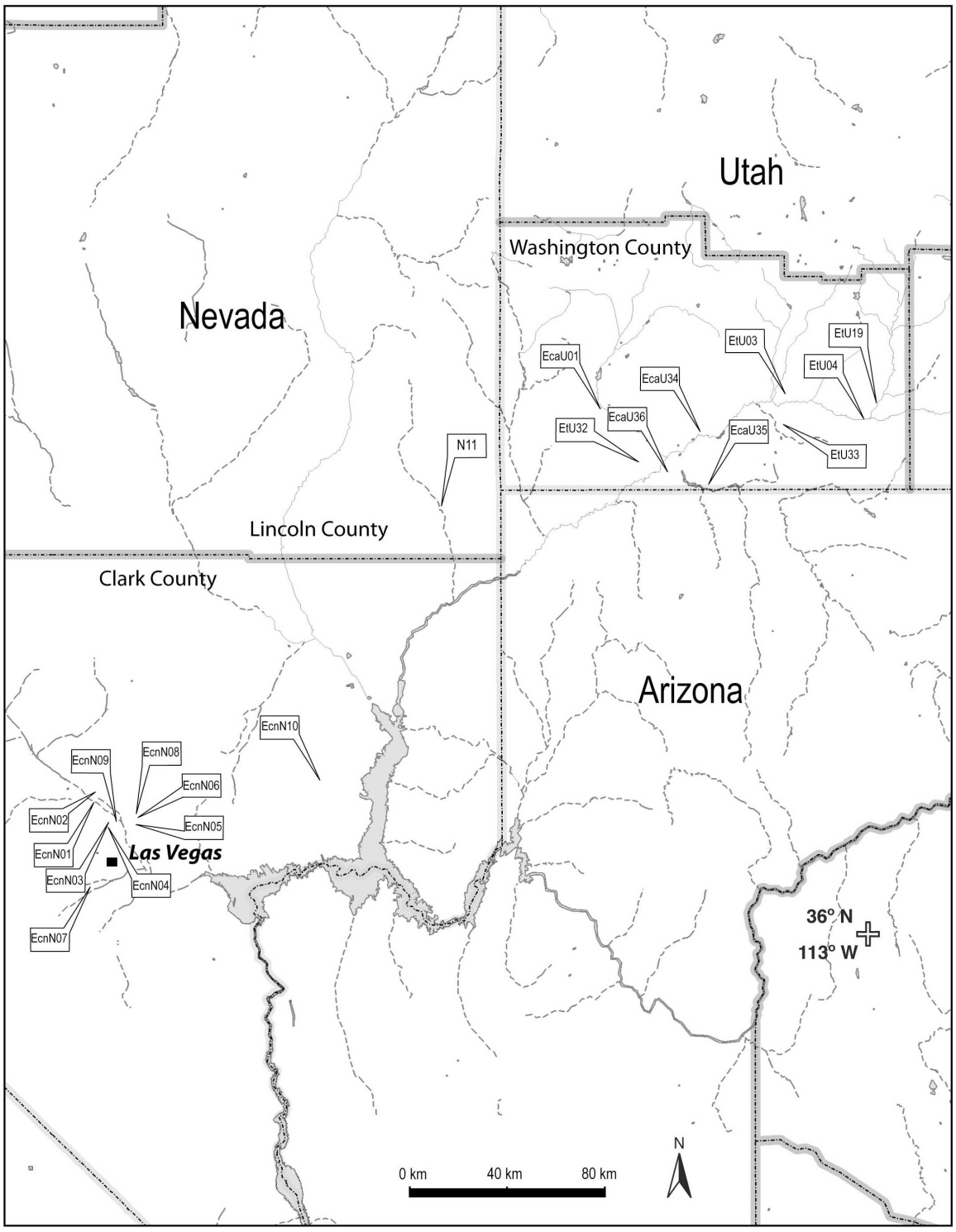

FIG. 3.2. Sites sampled in Clark County, Nevada (*E. corymbosum* var. *nilesii*), Lincoln County, Nevada (*E. corymbosum* N11), and Washington County, Utah (*E. corymbosum* var. *aureum* and *E. thompsoniae*).

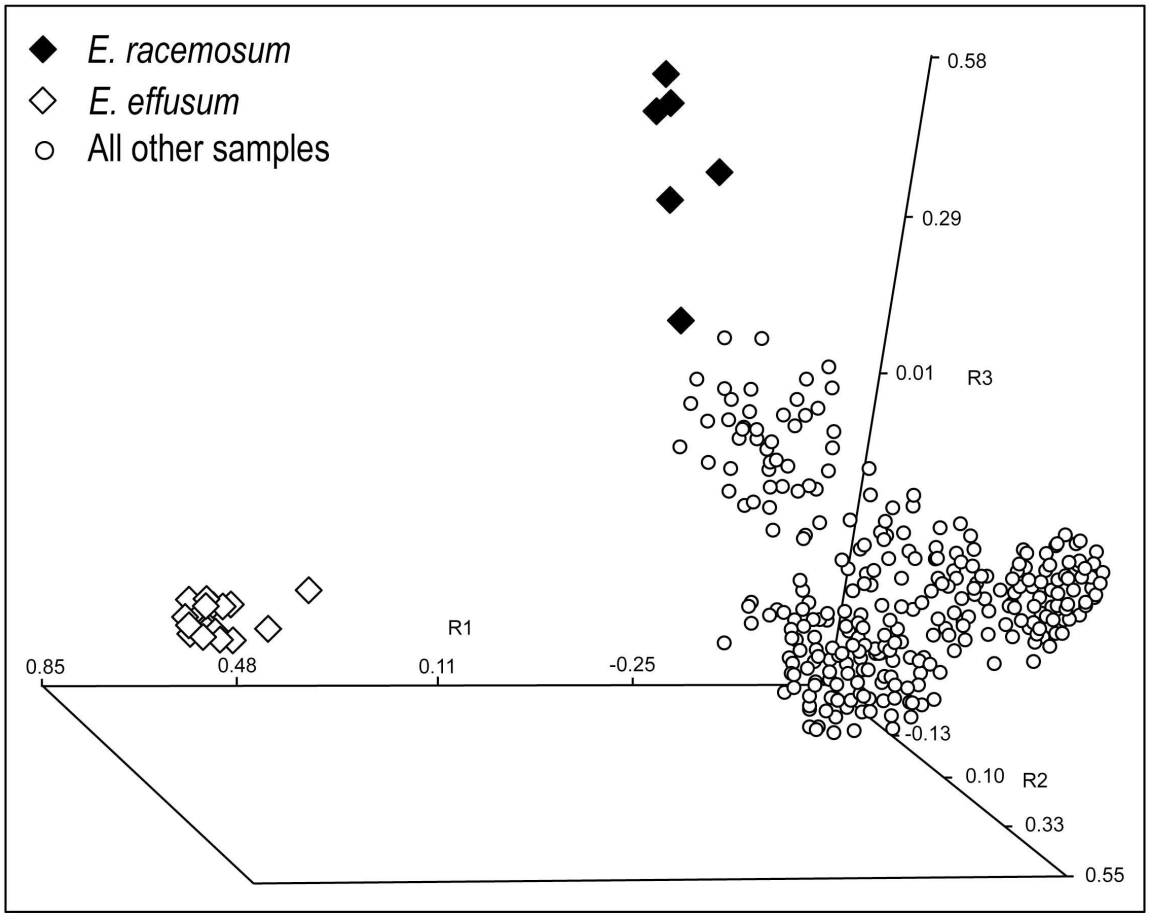

FIG. 3.3. PCA demonstrating the genetic divergence of *E. effusum* and *E. racemosum* samples from all others based on AFLP markers.

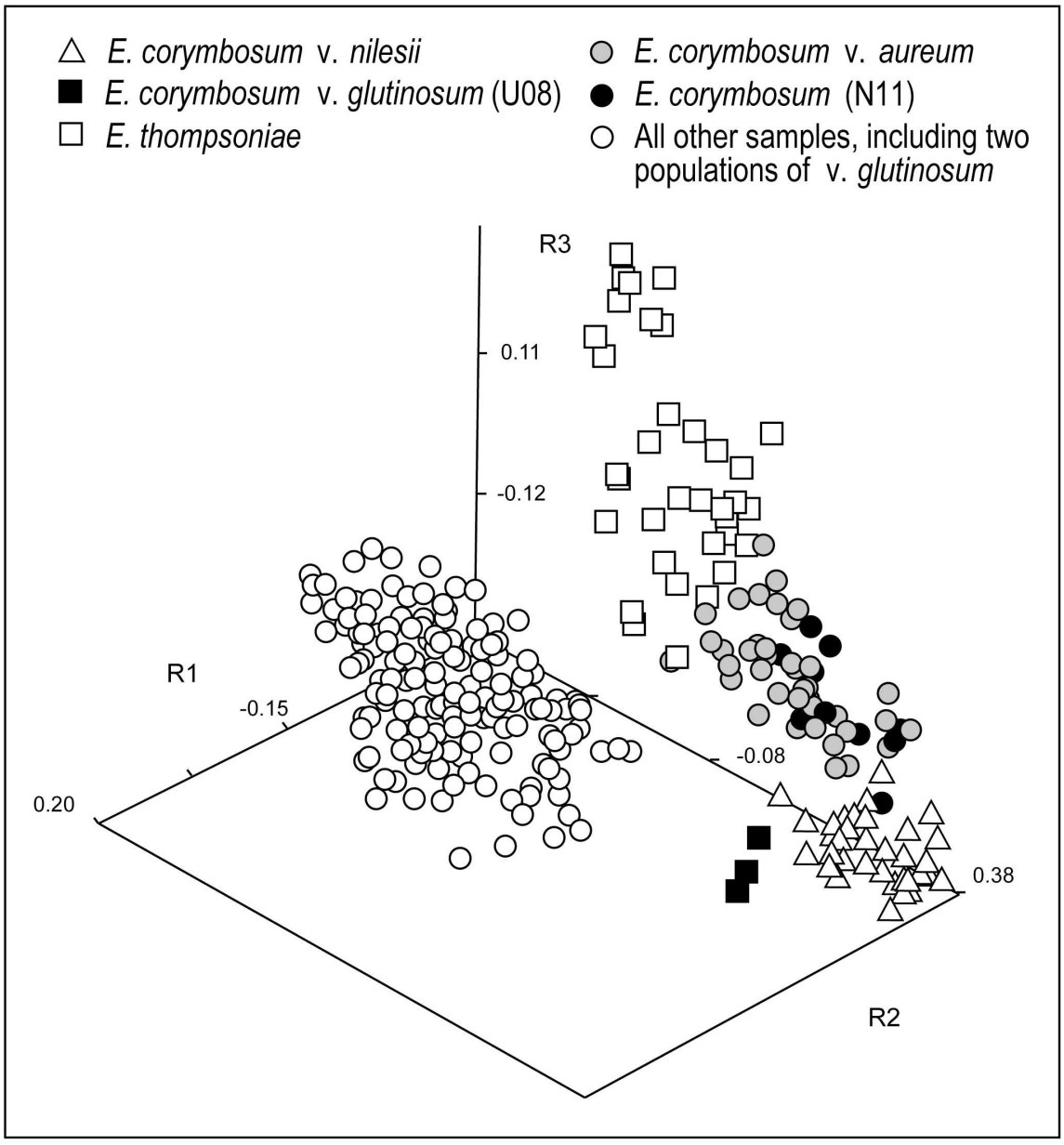

FIG. 3.4. PCA of samples of *E. corymbosum* var. *nilesii*, var. *aureum*, one population of var. *glutinosum*, and *E. thompsoniae* to each other and to all other samples tested based on AFLP markers. (Samples of *E. effusum* and *E. racemosum* were excluded).

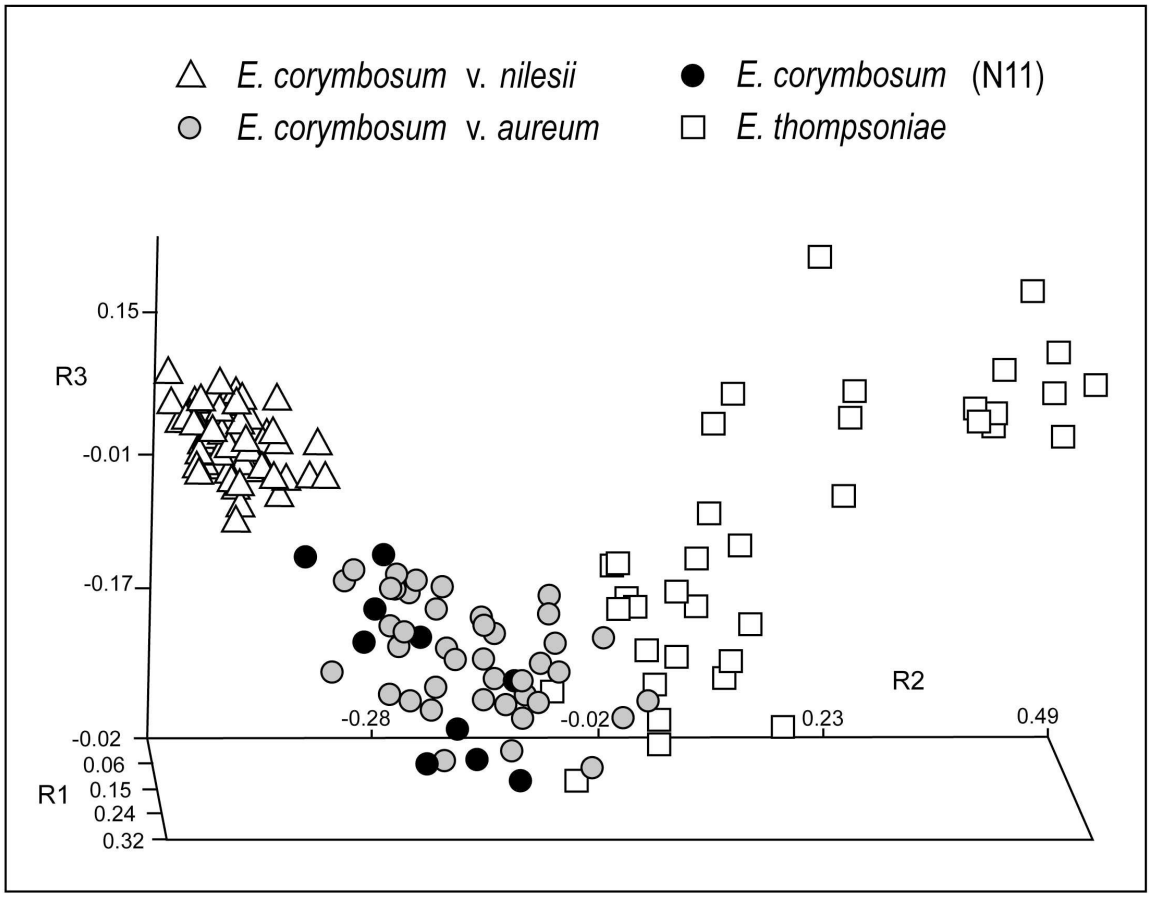

FIG. 3.5. PCA demonstrating relationship of *E. corymbosum* var. *nilesii* samples to the most closely related taxa – *E. corymbosum* var. *aureum* and *E. thompsoniae* – based on AFLP markers.

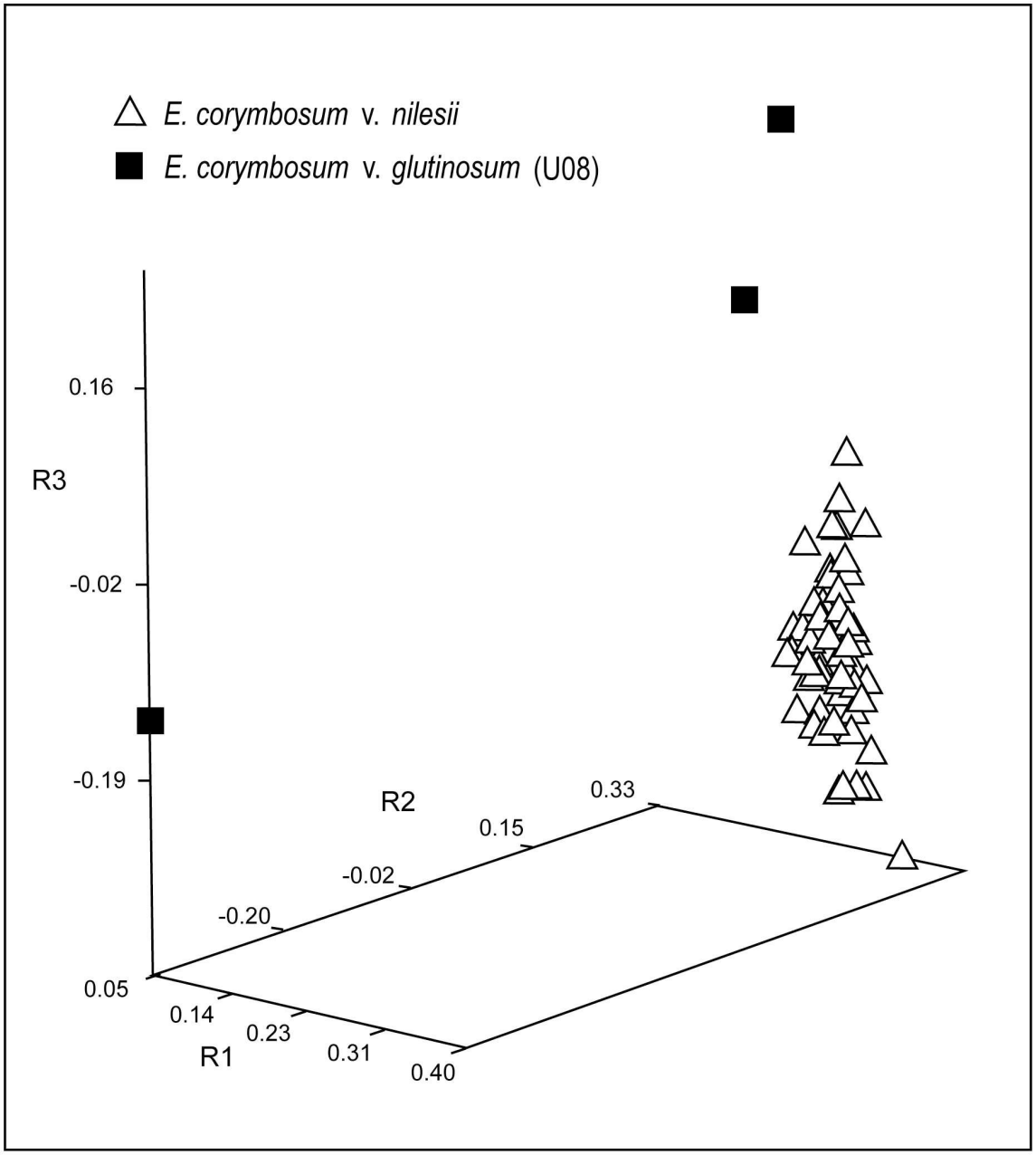

FIG. 3.6. PCA showing the relationship of *E. corymbosum* var. *nilesii* samples to three samples of *E. corymbosum* var. *glutinosum* (population U8).

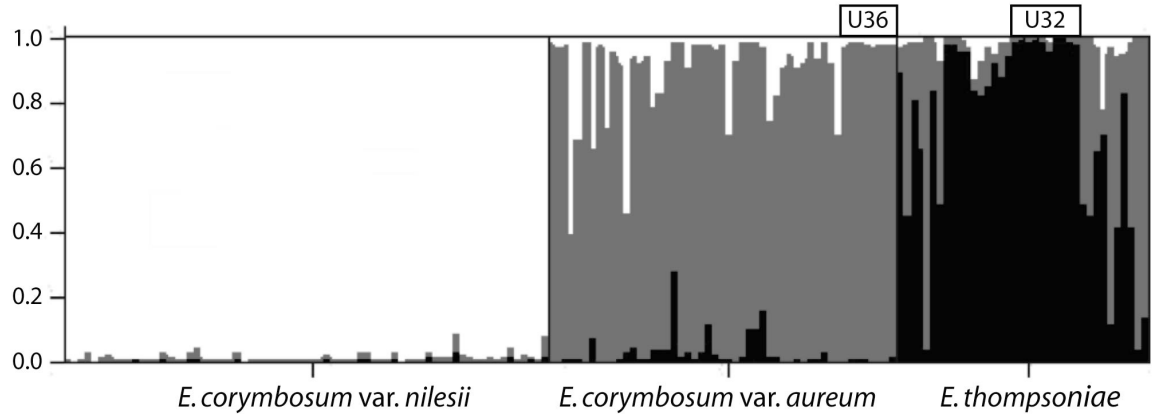

FIG. 3.7. Structure 2.2 bar graph of three taxa in order of populations sampled. Cluster membership is color coded, with white for Cluster 1 (corresponding to *E. corymbosum* var. *nilesii* populations N1-N10), gray for Cluster 2 (members of *E. corymbosum* var. *aureum* populations plus N11), and black for Cluster 3 (members of *E. thompsoniae* populations). Each bar represents an individual, with proportions of the 3 colors in each based on shared genetic profiles from the three clusters identified by Structure.

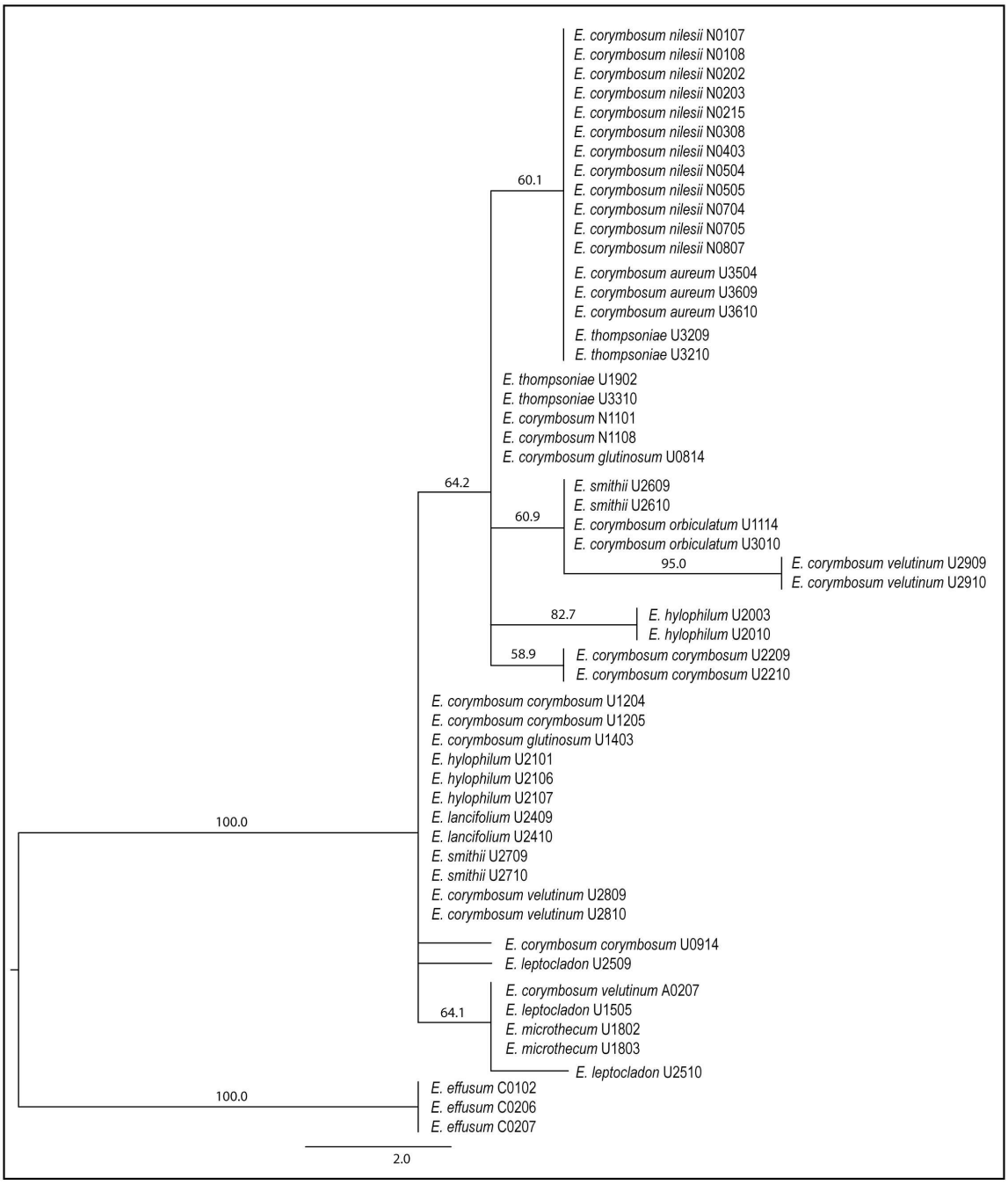

FIG. 3.8. Most parsimonious tree from a parsimony analysis of 13 *Eriogonum* taxa based on sequences of the *trnS/trnfM* cpDNA region. Branch numbers are bootstrap values.

CHAPTER 4

THE CENTER OF ORIGIN OF THE *ERIOGONUM CORYMBOSUM* COMPLEX: A BIOGEOGRAPHICAL ANALYSIS

ABSTRACT

The aim of this paper is to twofold: 1) to reevaluate the largely discredited center-of-origin model of biogeographical analysis by using it as a starting point to 2) examine the biogeographical distribution of the wide-ranging infraspecific complex *Eriogonum corymbosum* – the crispleaf buckwheat. The center-of-origin concept dates back to Darwin and earlier proponents. But it fell out of fashion with the increasing appreciation for vicariance as a mechanism for allopatry and subsequent speciation. Not long after plate tectonics became widely recognized, center-of-origin proponents had dropped to a mere handful and the concept has never regained its stature. I argue that it is a valid model theoretically, but the criteria used to identify a taxonomic group's center of origin can become increasingly less reliable over time. Evidence of a center of origin for a younger complex of taxa is more likely to be demonstrable, and examining such a group with this model can provide profitable insights, as I found with this investigation of buckwheat varieties.

INTRODUCTION

Center of origin concept

Eriogonum corymbosum is a wide-ranging, shrubby buckwheat species, distributed primarily across the Colorado Plateau. Two of the eight currently recognized

varieties (Reveal 2005), have become established beyond the Plateau. One of those, *E. corymbosum* var. *aureum*, is distributed across an ecotonal region between the Great Basin, the Colorado Plateau, and the Mojave Desert (Meyer 1978; McLaughlin 1989; Ricketts et al. 1999). Populations of variety *aureum* are found in and around St. George in Utah's southwestern corner (see Chapter 3). While these three ecological provinces have relatively sharp boundaries due in part to the geologic histories of their formations and the resulting topographical, edaphic, and climate differences, the shift from one to the other in the region around St. George is less clear. The second buckwheat taxon established outside the Colorado Plateau, the recently named variety *nilesii*, is found in the northeastern reach of the Mojave Desert where that province extends into the Las Vegas Valley of Clark County, Nevada (Reveal 2004). Here, I address the phylogeography of the *E. corymbosum* complex as a radiation of taxa from a putative center of origin, and in the context of a historical review of these three western physiographic provinces in North America.

In a genetic study of shrubby buckwheat taxa (see Chapter 3), evidence supported the nomenclatural change for populations of *E. corymbosum* in and around Las Vegas, Nevada, to variety *nilesii*. Since the complex is composed of infraspecific taxa, the divergence of member populations may be due to a process of dispersal and subsequent range expansion into regions with different ecological niches and selective regimes. This "dispersalist" view, with range expansion and potential allopatry that such a hypothesis entertains, has a checkered past. It was launched by Charles Darwin in his magnum opus of 1859 to explain the divergence of all taxa, and but eventually fell from grace, replaced by a view of vicariance biogeography that combined a cladistic approach to speciation

with an emphasis on vicariance as the mainspring of disjunct distributions (Wiley 1988). But Darwin's conceptual idea deserves another look.

Charles Darwin (1859, 1868) promoted a number of premises and hypotheses in fleshing out his theory of species evolution. Some of these have stood the test of time (e.g. natural selection) while others have been challenged (e.g. sympatric speciation, Mayr 1994) or even rejected outright (e.g. pangenesis, Provine 1971). In light of the fact that he was working without the benefit of Mendel's research or the yet-to-be explained plate tectonics, it is not surprising that some of his ideas would be less than accurate.

Darwin's view of dispersal, allopatry, and subsequent speciation was built upon a concept of centers of origin for related taxa (Darwin 1859). This concept contends that once a species arises and expands its range from a center of origin via dispersal, the probability that members will encounter geographic areas with different niches increases, along with concomitant new selective forces that will tend to promote divergence. Darwin viewed dispersal as the main mechanism for range expansion, which is a key element of speciation. He felt that the span of geologic time was great enough to allow levels of dispersal that have led to today's diverse biotas, including rare long-distance dispersal events (jump dispersal) such as transoceanic migration.

Although the idea gained support from many researchers, including the evolutionists George Gaylord Simpson and Ernst Mayr (MacDonald 2003) and the Soviet agricultural geneticist Nikolai Vavilov (Crow 1993), there were detractors from the outset. Joseph Hooker returned from an expedition to Antarctica and the adjacent continents in 1843 with specimens of plants that led him to conclude that some continents had not only once been joined, but had experienced quite different climates (Hooker

2008). Besides finding some of the same plant families and even genera in South America, Australia, New Zealand, and Tasmania, he found 77 plant species on these three continents, most of which were only found in this southern temperate zone. He correctly concluded these disconnected floras were once continuous on a single southern continent (which we now know was Gondwanaland) that had since become separated into the aforementioned continents. Instead of suggesting a radical theory of continents having drifted apart, Hooker argued that a drop in sea level would have connected two or more of the continents. Hooker was one of Darwin's closest confidants, yet neither Darwin nor his co-discoverer of evolution's mechanism, Alfred Wallace, agreed with Hooker. They assumed the taxonomic relationships were the result of long-distance dispersal rather than vicariance via geologic events (MacDonald 2003).

Hooker recognized several lines of evidence against transoceanic seed dispersal as the mechanism for this intercontinental distribution of taxa in the southern latitudes. He pointed out that some of those species with populations separated by oceans were very poor dispersers, yet other species that had effective wind dispersal mechanisms were not found on more than one of the continents. Darwin's erroneous over-reliance on dispersal may, in hindsight, seem imprudent. But given the information available at the time, transoceanic dispersal (for which there was strong evidence and obvious mechanisms) may have seemed considerably less improbable than mobile continents, (for which there was no direct evidence, and no known mechanism). As he maintained (Darwin 1859), "… our continents have long remained in nearly the same relative position…" The fact that he failed to recognize the contributions of vicariant events does not diminish the potential validity of his center-of-origin concept, since both long-distance dispersal or

continental breakup could fragment a once-cohesive geographic range of related taxa and thus obscure the location of a taxonomic group's origin. Although Darwin viewed continents as immovable, he was not so wedded to his dispersalist view of range expansion and speciation that he felt such centers of origin would remain eternally discoverable.

Darwin was well aware of "geographical and climatical changes which have certainly occurred within recent geological times" that "must have rendered discontinuous the formerly continuous range of many species." Thus, he was not naïve to the possibility of centers of origin having been lost over time. For that matter, he was wise enough to imagine "our ignorance with respect to former climatical and geographical changes" and that such changes must explain many of the anomalies of biogeography (Darwin 1859).

Recognizing that barriers to dispersal led to changes in floral and faunal communities, Darwin (1859) argued that the greater the barrier, the more dramatic the change: "We see this in the great difference in nearly all the terrestrial productions of the New and Old Worlds, excepting in the northern parts, where the land almost joins..." He recognized that different communities could develop within a single region due to barriers like mountain ranges or deserts, but since barriers were not as impassable as oceans, those differences would be considerably less dramatic than between communities on different continents. Thus, Darwin recognized the "deep organic bond" tying groups together in space and time was inheritance. While he understood that environmental variations and natural selection modified populations over time, and that vicariant events such as mountain building and glaciation could separate populations and lead to

speciation, a primary goal in The Origin was to emphasize that the overall similarities between taxa could be accounted for by inheritance.

Darwin also understood that some species have populations on more than one continent, although he admitted "extreme difficulty" in understanding how they achieved this. He was, however, confident that they could not have evolved twice, which he felt should be viewed as an untenable "agency of a miracle" (Darwin 1859). Darwin found that, in general, species that should not be capable of crossing oceans failed to do so, and he offered as evidence the fact that terrestrial mammalian species are typically confined to separate continents. So even though he recognized that long-distance migration could obscure the center of origin for a group of taxa, in general he found this concept sensible and obvious. Furthermore, he recognized this concept hierarchically, with families, subfamilies, genera, and species often confined to a single region.

Thus, for Darwin, the idea of a center of origin for related taxa was not so much a reliable theory of populations as it was an argument against the independent origin of species, which was still a popular concept at the time. The radical foundation of his theory of evolution was that all life is related, with each species having originated once, and in one place, yet descended from another. So his center-of-origin concept was a rational premise used to support his theory of evolution. But it appears that Darwin's over-reliance on a dispersalist model as a critical component of allopatric speciation, without acknowledging the importance of vicariant events, led to the near total dismissal of his center-of-origin concept today.

In 1902, Charles Adams, an advocate of Darwin's center-of-origin concept, described 10 criteria by which a taxonomic group's center of origin might be recognized

(Adams 1902). These criteria were later expanded upon and explained in detail by Cain (1944), three of which were, 1) the location with the greatest number of taxa or forms, 2) the location with the most closely related forms, and 3) the location with the least dependence on restricted habitats. Cain interpreted this last criterion to mean that "a species is more polymorphic at the center or origin" presumably because a restricted habitat would be occupied by a more narrowly adapted population.

By the mid 20th century, Darwin's center-of-origin concept had fallen out of favor. An effective blow was landed by the botanist Léon Croizat (1952, 1958) when he leveled the rational argument that repeated patterns of disjunct associations composed of very different organisms with dramatically different migratory capabilities would not be likely to have arisen by long-distance dispersal. Furthermore, Croizat was aggressive as well as creative, and the polemical nature of his attack on Darwin's center-of-origin concept had a condescending level of vitriol and disdain that may have been more effective than his unadorned arguments would have been alone. As he put it, "A science of dispersal is only as wide or as narrow as the preoccupations of those who entertain it. Those who look to it for a pleasant account of sundry theories and curious cases of distribution may rest satisfied with much less, of course, than those who intend to reach bottom in everything of nature they touch" (Croizat 1958).

Croizat instead offered his own theory of panbiogeography, which provided a vicariance mechanism for the separation of related communities and taxa found on different continents. Rather than recognize Wegener's (1929) mechanism of continental drift to explain evolutionary history in biogeographical terms, he instead initially surmised that land-bridges had existed that would explain the separation of entire groups

of related taxa whose populations had once been continuous (Lomolino et al. 2006). His theory thus dismissed dispersal as an unimportant mechanism and an unnecessary explanation for disjunct populations of species and other related taxa. Although most of the scientific community tended to ignore Croizat's work, interest in it by some did lead to the emergence of the more broadly accepted discipline of vicariance biogeography, which supplanted Darwin's dispersalist model and included Hennig's phylogenetics (Croizat et al. 1974; Briggs 2007). The broad acceptance of plate tectonics by the 1960s and 70s provided a powerful theoretical boost to vicariance biogeography, which further marginalized Darwin's dispersalist model, and with it, the concept of centers of origin (MacDonald 2003; de Queiroz 2005).

Ultimately, vicariance biogeography, or cladistic biogeography (Humphries and Parenti 1986), suffered a fall from grace similar to Darwin's dispersalist model for essentially the same reason – an over-reliance on a single mechanism for allopatry. The emergence of phylogeography in the 1980s, which gained momentum with the development of PCR technology in the 1990s, led to a torrent of phylogenetic research, which reestablished dispersal as an important mechanism for disjunct distributions, including those separated by oceans. The contributions of dispersal to biogeography have now, in the view of some (de Queiroz 2005), been put on an equal footing with vicariance as an agent of historical biogeography. But the center-of-origin model has not been lifted with it.

The marginalization of Darwin's centers-of-origin concept was due in part to the trivialization of his dispersalist model's contribution to allopatry and subsequent lineage divergence. The evidence for geological vicariance as a mechanism for allopatry,

particularly in regards to the contributions of plate-tectonic events, pushed the centers-of-origin concept further from consideration. But deep time has the potential to obscure the biogeographical evidence demonstrating a center of origin for monophyletic associations at higher taxonomic categories, regardless of the mechanisms that led to allopatry. However, for taxonomic groups with more shallow timeframes (such as intrageneric or infraspecific complexes), the likelihood that evidence for a center of origin can still be gathered should be considerably greater.

The *E. corymbosum* complex is just such an association of infraspecific taxa that might represent an ideal system for testing the concept of a center of origin. This complex of eight buckwheat varieties has populations distributed widely, but confined mainly to the Colorado Plateau. Two varieties have extended the range of the complex into two different ecological provinces – the Great Basin and the Mojave Desert. To consider the putative historical biogeography of the *E. corymbosum* complex, some background on the ecological provinces within which its members are found is in order.

Relationship of plate tectonics to physiographic and floristic provinces

Two major physiographic provinces – the Basin and Range and the Colorado Plateau – dominate the arid regions of southwestern North America. These two continental subdivisions have similar origins, but the geologic fortunes of the Basin and Range took a dramatically different turn in the Miocene resulting in a vastly different 20-million-year history (Coney 1983; Hunt 1983). Both provinces are part of an enormous Cenozoic geanticline extending from east of the Rockies nearly to today's Pacific Coast. Both provinces experienced uplift until the western flank of that geanticline collapsed,

forming today's Basin and Range. The Colorado Plateau has remained remarkably stable geologically, suffering for the most part only the slings and arrows of weather and erosion as it continued to rise. The engine beneath the uplift of both regions and the eventual faulting of the Basin and Range is plate tectonics.

From the Precambrian to the mid-Paleozoic, North America was a low, cratonic platform with its western edge ending in part along what is now western Arizona, the Colorado Plateau's western margin, and essentially the western borders of Wyoming and Montana (Coney 1983). West of that was a broad continental shelf covering what would be southern California, eastern Nevada, and all of Idaho. During the Jurassic, the Atlantic Ocean and the Gulf of Mexico opened, freeing North America from Africa and most of South America. By the late Cretaceous, the Pacific, Farallon, and Kula tectonic plates paved the Pacific Ocean, and a trench had formed along North America's western margin. Spreading from the East Pacific Rise, the Farallon plate plunged into the trench, subducting beneath the continental plate, and by the end of the Oligocene, the Rise itself had reached North America's westward-moving margin. This created strike-slip transform faults between the northwestward-moving Pacific plate and the continental plate, ceasing subduction along this transform boundary. This collision of the East Pacific Rise with North America set the stage for the Basin and Range rifting that would occur during the Miocene. By the end of the Miocene, the transform margin had moved inland, opening up the Gulf of California and creating the San Andreas transform system.

During the Paleogene Period of the Cenozoic Era, the regions that would become the Colorado Plateau and Basin and Range had similarly low elevations (Morris and Stubben 1994). Both regions were raised some three kilometers. But during the

Miocene, while the Colorado Plateau remained uplifted, the crust beneath the Basin and Range spread dramatically, east and west, causing the land to break into great blocks, and this extensional faulting has continued to the present. Although theories explaining the causes for this crustal spreading beneath the Basin and Range are still debated, there is general agreement that extensional tectonism is due to interactions between the Pacific, Farallon, and North American plates (Atwater 1970; Coney 1983; Dickinson 2006). In one view, the subduction of the Farallon plate beneath the over-riding continental plate generated plumes of rising heat from the mantle that bowed the crust into an arc, stretching the rigid continental crustal material until it faulted into a series of tilted valleys and parallel ranges (Stewart 1971). In another view (Dickinson 1979; Dickinson and Snyder 1979), as the continental plate overrode the Farallon plate along with the rise from which it spread, the subducting Farallon plate became detached from the former spreading center. As the detached plate moved down into the mantle, the widening gap (a "slab window" where the spreading center had once been) allowed an upwelling of heat (generated by the subducting plate) beneath the Basin and Range region with the same results of the aforementioned hypothesis.

While the Basin and Range has been stretched and faulted over the last 17-20 million years, the Colorado Plateau region has remained relatively intact. The crust beneath it is nearly 40km thick, as opposed to the 25km crust beneath the Basin and Range (Coney 1983). A plate-tectonic model to explain the Plateau's uplift suggests that during the early Cenozoic era, part of the Farallon plate became fused to the continental plate, and by the mid-Cenozoic it became detached beneath the Colorado Plateau. As the delaminated section of plate sank it was replaced by rising and expanding lithospheric

material that lifted the crust in this region dramatically (Bird 1984; Beghoul and Barazangi 1989). While it continues to rise, its surface continues to erode.

The onset of the Basin and Range's faulting led to today's ranks of parallel mountain ranges and basins for which the province is named. As one end would drop, the high end of each of the tilting blocks would form a steep north-south trending mountain range. The down-sloping side of the blocks formed basins that eventually ended where a lower end would butt up against the raised end of the next block. With time and erosion, the basins have filled with sediment, creating depositional valleys.

The Basin and Range's northern section (covering much of western Utah nearly all of Nevada) is a cold desert called the Great Basin – an internally drained region from which no water escapes. During the spring, most of the melting snow and any rainwater evaporates, while the rest either sinks as ground water or collects into ephemeral playa lakes. The faulted mountains and deep, sediment-filled basins in this harsh and arid landscape prevent the formation of a river system that might reach the sea. So instead of being carried away as runoff, sediments accumulated, filling the basins to depths that can exceed 4,500 meters.

Because the Colorado Plateau escaped serious faulting and maintained its elevation, it has become an excavated province rather than a depositional one. Rather than an internally drained landscape, it is well drained by the Colorado River and its tributaries. The raised relief of the Plateau is cut and carved by its streams and rivers. This drainage system effectively carries away the work of erosion, creating a landscape with a great variety of exposed parent material.

The differences between these two physiographic provinces have led to ecoregions that are floristically different as well. The entire Colorado Plateau physiographic province is generally considered a separate ecoregion while the Basin and Range physiographic province is usually subdivided into a number of ecoregions, including the Great Basin and the Mojave Desert (Cronquist 1978; MacMahon 1979; McLaughlin 1986; Ricketts et al. 1999). McLaughlin's (1986) distributional factor analysis of 50 floras found throughout the Basin and Range and Colorado Plateau produced six floristic "elements," three of which were the Great Basin, Colorado Plateau, and Mojave Desert. The Great Basin element was allied floristically with more northern, mesic floras, while the Mojave Desert and Colorado Plateau were only weakly correlated with peripheral regions and had high degrees of endemism. An examination of North American ecoregions by Ricketts et al. (1999) produced similar results.

The Colorado Plateau has the highest elevation of the three ecoregions, at generally over 1,500 meters. It has cold winters, and during the summer the days are hot and nights are cool. The average annual precipitation is 510mm. The Great Basin ecoregion, besides its very different depositional geologic character, is also lower in elevation and drier than the Colorado Plateau. Its basins are generally between 1,220 and 1,500 meters, and it receives less than 250mm of precipitation annually. The Mojave is lower still, lying mostly between 610 and 1,220 meters, and averaging 65-190mm precipitation annually. Although it shares a similar geologic history with the Great Basin, its lower latitude, elevation, and precipitation clearly set it apart as a separate ecoregion (McLaughlin 1986; Ricketts et al. 1999).

Since the evolution of angiosperms during the lower Cretaceous, these physiographic provinces have changed floristically during their geologic transformation. By the Miocene, most modern genera were present in southwestern North America (Cronquist 1978), and the boundary between the Great Basin's cold-desert flora and the Mojave's warm-desert flora developed at this time. Cronquist (1978) suggests that *Eriogonum* appears to have been derived in western North America, and pollen grains considered to be *Eriogonum* were found from the Quaternary (Reveal 1978). The concentration of *E. corymbosum* populations and taxa in the Colorado Plateau (Albee et al. 1988), with a more limited number of sites in the Mojave and Great Basin, suggests a Colorado-Plateau center of origin.

Objectives

The diversity and wide distribution of the *E. corymbosum* complex, and the low taxonomic level of its infraspecific relationships, make it a useful group with which to examine the center-of-origin concept. In the process of doing so, I hope to shed light on the historical biogeography of this taxonomic assemblage. To accomplish these objectives, I will examine sampled populations in the *E. corymbosum* complex with the previously mentioned criteria described by Adams (1902) for identifying a center of origin. Populations will be tested and compared for genetic diversity to evaluate the criterion that more diverse populations will be nearer the center of origin while populations with less diversity will be further from the center. The ranges of the varieties will be compared since the center-or-origin model suggests that a greater density of taxa should be found nearer the center of origin (Adams 1902; Cain 1964).

MATERIALS AND METHODS

Thirty-one *E. corymbosum* sites were sampled, which included six varieties (*aureum, corymbosum, glutinosum, nilesii, orbiculatum,* and *velutinum*). DNA was extracted and AFLP profiles were developed for individuals from each population (see Chapter 2 for collection, DNA extraction, and AFLP methods). I generated a map of the sample sites, overlaid with the borders of the major geologic provinces in this region (Fig. 4.1).

To examine the *E. corymbosum* complex for a possible geographic center of origin, I chose to test three criteria for recognizing a center of origin. The first two criteria suggest that populations or taxa near the center of origin for the complex will be more diverse. To measure population diversity, the program AFLP-SURV version 1.0 (Vekemans 2002) was used to obtain an allele-frequency based analysis. AFLP-SURV starts by estimating allelic frequencies in an AFLP data matrix for each marker locus in each population on the assumption that the markers are dominant and have only two allelic alternatives per locus (absence or presence). The program does this with a Bayesian algorithm that assumes a non-uniform prior distribution of allele frequencies (Zhivotovsky 1999). Based on these frequency estimates, the program then calculates population diversity via the approach of Lynch and Milligan (1994), measuring genetic diversity based on the average expected heterozygosity of the marker loci. This produces the diversity index *Hj* (Nei's gene diversity) for each population.

To compare and contrast population diversity, ArcGIS Desktop 9.3 (ESRI New York, esri.com) was used to create an interpolated distribution of populations and their

relationships across geographic space. Based on interpolation functions in the inverse distance weighted model (IDW), the program creates a continuous prediction surface from sampled point values (i.e. Nei's gene diversity). With this approach, an isocline map can be developed that combines sample diversity with latitude and longitude coordinates for all sampled populations to examine possible regional trends in population diversity (see Table 4.1).

To examine the taxonomic relationships of the *E. corymbosum* complex on a broad geographic scale, I mapped polygonal boundaries circumscribing known sites for each *E. corymbosum* variety (Fig. 4.3a). Sites and range information were gathered from herbarium specimens, floras, field surveys, and communication with field botanists. These generalized boundaries of the ranges for each variety allow one to visually examine the overall range of the species, the spatial relationships of the individual ranges to one another (including its peripheral regions as well as areas of overlap with two or more varieties), and the relationships of all these aspects to the major ecoregions.

RESULTS

Figure 4.1 gives the locations of all *E. corymbosum* sites sampled, and their distribution within three different physiographic provinces – the Colorado Plateau, Great Basin, and Mojave Desert. Of the six varieties sampled, four are distributed mainly within the Colorado Plateau. Populations of variety *aureum* are distributed across an ecotonal region between the Colorado Plateau, Great Basin, and Mojave Desert, while the known populations of variety *nilesii* are all located in the Mojave Desert in Clark County, Nevada.

The generated diversity indices (*Hj*) for 31 populations of *E. corymbosum* (including six varieties) are listed in increasing order in Table 4.1. The least genetically diverse populations were predominantly variety *nilesii*, while the populations with the highest genetic diversity were variety *aureum*.

For each sampled population, the diversity index *Hj* was combined with latitude and longitude to create an interpolated distribution map (Fig. 4.2). Predicted regions of diversity are shown as color-coded contours across the sampling area based on sample-population diversity. Three regions showed increased diversity, which I circled. Two of these included more than one sampled taxon, while the third (in southwest Utah) included only variety *aureum*.

From the boundaries displayed in Figure 4.3b, it can be seen that variety *glutinosum* is broadly distributed in, and essentially confined to, the southwestern Colorado Plateau region. The northern extension of its range overlaps with varieties *corymbosum*, *orbiculatum*, and *revealianum*. Also confined nearly entirely to the Plateau are varieties *orbiculatum* (central Plateau), *corymbosum* (northern Plateau), *revealianum* (mainly eastern Plateau), and *heilii*. Variety *revealianum* has a limited range and spotty distribution, and is only marginally distinct from *corymbosum*, while variety *heilii* is known only from a single location signified in Figures 4.3a-d by a small yellow circle with a black border (Reveal 2005). Variety *orbiculatum* is very distinctive with its orbiculate to heart-shaped leaves, and overlaps the ranges of varieties *corymbosum* and *velutinum*. Variety *velutinum* has a range that extends from the central Colorado Plateau to its eastern boundary and beyond into Colorado and New Mexico.

The range of variety *aureum* is on the western periphery of the overall range of the *E. corymbosum* complex, and some of its populations are the most genetically diverse of all those sampled (Table 4.1, Fig. 4.2). The Shivwits population in particular, considered until the study presented in Chapter 3 and this study to be the only verified *aureum* population (Reveal 2005), is the most diverse of all the sampled *aureum* sites.

The known range of variety *nilesii* is entirely within the Mojave Desert within Clark County, Nevada. This peripheral taxon, unlike variety *aureum*, does support the criteria for the center-of-origin model. Suspected populations (untested genetically) are also found within the Arizona Strip region of Mohave County, Arizona. Whether these are more closely allied with variety *aureum* or *glutinosum* will remain unanswered until genetic analyses can be done. Until such confirmation, I have extended the range of variety *nilesii* into Arizona.

In light of the overlapping ranges of varieties presented in the range map, and to look for possible correlative information, I overlaid the circles that circumscribed areas of genetic diversity (from Fig. 4.2) onto the varietal-range map (to produce Fig. 4.3c). Two of the circular areas of within-population genetic diversity coincide well with areas of regional taxonomic diversity. To pursue this line of inquiry further, I circumscribed an area defined by the two circles of within-population genetic diversity to produce a putative center of origin (Fig. 4.3d).

DISCUSSION

With this reexamination of Darwin's (1859) center-of-origin concept, I found intriguing correlations that, when taken together, delineate a potential geographic region

in which *E. corymbosum* may have originated. However, the criteria for Darwin's model of dispersal and divergence from a central location, as described by Adams (1902) and later clarified by Cain (1944), did not provide a simple or narrowly defined center of origin for the *E. corymbosum* complex, even at this low taxonomic level of infraspecific taxa. Although some of the applicable criteria have clearly been met, others are not so clear. I will argue that these mixed and apparently conflicting results paint a complex picture, yet they can still be interpreted to suggest a center of origin. Although further investigation is needed, these findings provide interesting inferences that may explain parts of the biogeographic puzzle and generate hypotheses for further investigations.

The distribution of *E. corymbosum* varieties sampled for the study in Chapter 3 suggested the possibility of biogeographical relationships that prompted the investigation here. The majority of varieties were sampled from the Colorado Plateau (Fig. 4.1), and those populations tended to be more closely related to each other than to two varieties with peripheral ranges located on the border or off the Plateau. To investigate this, the AFLP data of the sampled populations of these six varieties were examined for within-population genetic diversity with the index *Hj*, the results of which provided more intrigue when three regions of population diversity were revealed (Fig. 4.2). One might argue that, with three regions of allelic diversity demonstrated rather than one, the center-or-origin model was not supported since the criterion of a center of diversity was violated. Furthermore, the three regions of diversity spanned the latitudinal range of the sampled populations. To look at this further, a better understanding of the ranges of *E. corymbosum* varieties was needed, and the range-area maps were generated to address this.

A number of inferences are evident from the mapped polygonal area-ranges of the *E. corymbosum* varieties (Fig. 4.3a-b). First, there appears to be a center of taxonomic diversity in southern Utah. Second, there are two peripheral and possibly somewhat disjunct taxa (varieties *aureum* and *nilesii*). Third, most of the varieties are confined to the Colorado Plateau, with the exceptions of peripheral ranges of *aureum* and *nilesii*, and part of the range of *velutinum*. And fourth, there are two general areas of taxonomic diversity where the ranges of three or more varieties overlap. Finally, if one looks at the ranges more inclusively, there is a broad area of overlap that includes six of the eight currently recognized varieties.

In light of the two different approaches to mapping distributions of populations, I combined the information from Figures 4.2 and 4.3a to compare different aspects of diversity (Fig. 4.3c): 1) taxonomic diversity demonstrated by areas with overlapping ranges of varieties, and 2) allelic diversity within populations (regions within the black circles). Both of these attributes are demonstrations of diversity that support the criterion of a center of origin (Adams 1902; Cain 1944). The resulting map provides corroborative insight into the organization of these taxa. The two general areas of taxonomic diversity demonstrated in the range map coincide geographically with the overlaid regions of within-population genetic diversity (Fig. 4.3c). The region of within-population genetic diversity in central Utah circumscribes one of the regions of taxonomic diversity, encompassing four varieties (*corymbosum*, *orbiculatum*, *revealianum* and *glutinosum*) with a fifth nearby (*heilii*). The southeastern region of within-population genetic diversity circumscribes the other, with three varieties circumscribed (*corymbosum, orbiculatum,* and *velutinum*). This alignment of two very different aspects of diversity

provides corroboration for these as centers of diversity. By using the two within-population sites of allelic diversity to define a broader circular region (Fig. 4.3d), the overlap of all taxonomic varieties (with the exceptions of *aureum* and *nilesii*) are circumscribed in a single region of diversity.

The third area of within-population diversity, demonstrated in the isocline map (Fig. 4.2) in southwestern Utah based on the IDW model, is not corroborated by a region of taxonomic diversity, as only the single variety *aureum* is represented. The area in and around St. George, Utah, where these populations of variety *aureum* are found, is peripheral to the range of the complex and would be expected, based on the criteria for the center-of-origin model, to be less diverse. Although the region is less diverse taxonomically, with no overlap between the range of *aureum* and any other *E. corymbosum* varieties, its high within-population diversity strays from a principle criterion of the center-of-origin model. Again, rather than discard the model due to an apparent failure of populations on the ground to demonstrate the criterion of reduced diversity, these apparent contradictions were intriguing, and demanded further investigation.

As suggested in Chapter 3 and by others (Welsh et al. 2003; Reveal 2005), variety *aureum* might have been derived from an association with the species *E. thompsoniae*. The possibility of hybridization was worth investigating, since introgression could spike the allelic diversity levels of an otherwise young taxon on the periphery of the complex. The center-of-origin model suggests that the location of *aureum* populations on the periphery of the *E. corymbosum* complex is evidence for its relatively recent divergence, but its high levels of allelic diversity contradict the precepts of this model. Thus,

interspecific hybridization provides a possible explanation for the anomaly of high allelic-variation levels found in some *aureum* populations. The alternative explanation – of an older taxon with high genetic diversity on the periphery of a species complex – conflicts with the center-of-origin model of taxonomic distribution. The cpDNA sequence findings in Chapter 3 demonstrated that some individuals of variety *aureum* and *E. thompsoniae* shared the same haplotype, giving further evidence to support the presumption of hybridization between these two taxa.

Due to this unexpected result of a single peripheral variety with high within-population gene diversity, I examined the AFLP data with hybridization in mind. Allele frequencies were calculated from the presence or absence of AFLP fragments for each population, and the mean frequency was computed for each taxonomic variety. Loci that may indicate evidence for hybridization/introgression among *E. thompsoniae* and *E. corymbosum* varieties *aureum* and *nilesii* are listed in Table 4.2. In this process, several loci were found that demonstrate an additive effect of bands suggesting that *aureum* may well have originally been a migrant of *nilesii*, now introgressed with *thompsoniae*. For instance, the alleles for a number of loci are rare in all taxa except varieties *nilesii* and *aureum* and the species *E. thompsoniae.* Three of those alleles are found in *E. thompsoniae* and variety *aureum*, five are found in varieties *aureum* and *nilesii*, and three more alleles are found in all three taxa. The alleles present at six of these loci support the hybridization of *aureum* and *E. thompsoniae*, and the five shared by *aureum* and *nilesii* suggest the possible derivation of one from the other.

These data suggests that variety *aureum* is derived from *nilesii*, and *aureum* populations are now (or have been) interbreeding with *E. thompsoniae* individuals. Thus,

variety *aureum* may well represent the initiation of a new center of origin for an incipient species. This evidence and the findings in Chapter 3 suggest that the genetic diversity of these populations is not due to having had a greater amount of time to diversify and expand in numbers than other varieties, but is due instead to a hybrid origin between *E. corymbosum* migrants (most probably variety *nilesii*) with *E. thompsoniae*. This putative interspecific origin would explain the otherwise unexpected combination of variety *aureum*'s presumed recent origin, limited distribution, lack of range overlap with other varieties, and peripheral location along with its higher within-population genetic diversity demonstrated here. The relatively distant genetic relationship between *aureum* and all taxa but variety *nilesii* and *E. thompsoniae* shown in Chapter 3 also supports this scenario.

In light of the explanation for the diversity of variety *aureum*, the overall findings for the *E. corymbosum* complex align well with Adams' (1902) applicable criteria for the center-of-origin model. Cain (1944) clarified Adams' criterion "*location of greatest differentiation of type*" to refer to "biotypes, subspecies, species, sections, etc." So this criterion can be viewed at multiple levels, particularly in regard to time. Both Adams and Cain suggest that the region of origin will have a greater diversity of forms than any comparable area peripherally. Like spokes on a wheel, the density of radiating taxa is expected to decrease with distance from a center of origin. Although not a picture of concentric uniformity, the overall picture of taxonomic range distribution in the *E. corymbosum* complex does demonstrate this tendency if one recognizes the center of origin depicted in Figure 4.3d. Again, the theoretical construct that suggests evidence for a taxonomic group's center of origin persisting through time is just that – a model by

which one can begin to asses the group's biogeography. The complexities of ecological diversity that include the panoply of community variants, edaphic diversity found throughout a region like the Colorado Plateau, along with dramatic variations in elevation and aspect, along with geologic and hydrologic diversity, all conspire to prevent a simple distribution of individuals, populations, and taxa predicted by the model.

At the level of biotypes, the criterion of within population diversity was not clearly met since two regions of diversity (disregarding the third already discussed in southwestern Utah) were distinguished within the larger central region of taxonomic diversity. Although I have not examined these two regions more closely, the next step would be to look for factors that would result in this apparent departure from the uniform predictions of the model. Perhaps a history of hybridization is involved, as appears to be the case for variety *aureum* in southwestern Utah. Or perhaps this double center is the result of landscape variation. It is worth noting that these two regions are found approximately equidistant from the Colorado River. Perhaps the river acts as a barrier, maintaining a level of allopatry that can lead to divergence of new taxa on either side (in this case variety *velutinum* to the east, and *revealianum* to the west). Then again, the river may act as a corridor to dispersal, possibly having helped the original taxon spread across the Colorado Plateau and assisting in the radiation that has led to the present complex of taxa. Like the Hardy-Weinberg principle, the center-of-origin model provides a starting point to examine the biogeography of a biological complex, particularly those composed of lower taxonomic entities. And it is the divergence from compliance with the model's criteria that demand attention.

In the *E. corymbosum* complex, the southern portion of the range of variety *corymbosum* encompasses parts of the ranges of all varieties but *aureum* and *nilesii*. When taken as a unit, this region of overlap also encloses the two of the three centers of diversity demonstrated in the isocline map (Fig. 4.2). The circle in Figure 4.3d is defined by the central and eastern regions of within-population diversity from Figure 4.3c. It would be worth examining variety *corymbosum* as a possible progenitor of the complex itself, if such a taxon still exists. In this regard, on approach might be to compare genetic markers in order to identify plesiomorphic traits that would either support or challenge the contention that variety *corymbosum* may have given rise to more recently diverged taxa.

When considering the criterion, "location of least dependence on a restricted habitat" (Adams 1902), the expectation is, as suggested for the wide-ranging variety *corymbosum*, that more generalist taxa or more similar taxa will be located closer to the center of origin. Three other varieties besides *corymbosum* (*orbiculatum*, *glutinosum*, and *velutinum*) also have broad ranges, each of which partly resides in the putative center of origin depicted in Figure 4.3d. In this regard, the arrangement of tested individuals from six *E. corymbosum* varieties analyzed via a principal components analysis of AFLP data shown in Chapter 3 suggests that these same four taxa – varieties *corymbosum*, *orbiculatum*, *velutinum*, and *glutinosum* – are more closely related to one another than to either of the two peripheral varieties *aureum* and *nilesii*.

Conversely, the regions in which *aureum* and *nilesii* are found may well be more restrictive habitats, with *aureum* found in the transitional zone between the Great Basin, Colorado Plateau, and Mojave Desert, and *nilesii* entirely within the Mojave Desert.

Their relatively small ranges, compared with the other four varieties, also may attest to their more recent origin. If this is indeed the case, they would presumably, as more recently derived taxa, be in an earlier phase of range expansion and selective adaptation to local conditions. As demonstrated in Chapter 3, these two taxa are also the most genetically distinct varieties. Although interspecific hybridization is very likely involved with the divergence of variety *aureum*, contributing to the high degree of gene diversity found among *aureum* populations, this is definitely not the case with variety *nilesii*, whose populations form a tight unit of low gene diversity (Fig. 4.2, Table 4.1).

In this examination, the genetic diversity levels within *nilesii* populations are so low relative to the other taxa in the complex that the colored contour map predicting regional genetic diversity clearly isolates the peripheral *nilesii* region (Fig. 4.2). Perhaps the selective forces within the Mojave are demanding to the point that, although gene diversity is low, the divergence that does occur within *nilesii* individuals persists due to its adaptive value. Another factor could have been the size of the founding population, which may have been the small remnant of a retreating generalist population, such as variety *glutinosum*, being driven back to higher ground and more northern latitudes with the heating and drying of interglacial periods. Although this is all speculation, with the peripheral isolate *nilesii* appearing to conform to the predictions of the center-of-origin model, the uniqueness of this distal taxon demands attention and further investigation. This demonstrates a value of the model, since compliance with it (as well as deviations from it) can generate hypotheses that warrant further investigation.

If variety *nilesii* is in fact a derivative of one of the taxa located on the Colorado Plateau, the range map may shed light on this, as yet unknown, taxon. The most

parsimonious routes to the Mojave from the presently known distributions would be from either variety *aureum* or variety *glutinosum*. Given that *aureum* may, like *nilesii*, be more recently derived (given the reasons above), variety *glutinosum* appears to be the most likely candidate. It could be the progenitor of either *nilesii* or *aureum*, or both. In Chapter 3 it was shown that three individuals from one population of variety *glutinosum* were more closely related to variety *nilesii*, supporting this possible past connection. Although they considered long-distance dispersal a possibility, that mechanism seems far-fetched given that *E. corymbosum* seeds do not have adaptations for long-distance dispersal. With the benefit of the range maps, it is readily apparent that variety *glutinosum* is the most proximal and thus the most probable progenitor of variety *nilesii*. And the range maps show *nilesii* to be a good candidate for the progenitor of *aureum* as well.

Although it could be a coincidence that this most-distal taxon of the *E. corymbosum* complex is composed of populations that are the least diverse of all those tested, the correspondence of *nilesii*'s peripheral location and lack of diversity seems more than coincidental. The other most distally collected populations were all well within the range limits of the complex, so their higher degrees of genetic diversity were in compliance with the center-of-origin model.

The center-of-origin concept at low taxonomic levels seems to be a useful, although exploratory, model with which to examine historical biogeography. Although the criteria were developed before the recognition of dramatic processes that can lead to vicariant dismantling of centers of origin (not to mention before a clear understanding of genetics or the discovery of DNA had been achieved), that historical reality need not be a

reason to disregard the center-of-origin model. The reality of sever vicariant events, such as those caused by plate tectonics, certainly complicates the application of the model. Therefore one must always be alert for deviations from the model since they may provide clues to hidden but dramatic events -- particularly at deeper levels of taxonomic hierarchy. With vicariance in mind, and the need for a more nuanced approach, the center of origin model can be used and adapted to help discover and explain findings that appear to stray from the model. For instance, in the present exploratory study, the possible influence Pleistocene climate oscillations and may provided the vicariant influence that led to the disjunct Mojave populations of variety *nilesii* during migratory advances and retreats of Colorado Plateau taxa.

The apparent hybrid swarm in southern Utah that appears to be guiding the evolutionary development of variety *aureum* is an instructive addition of complexity to the center-of-origin model at a low taxonomic level, demonstrating both the potentially rapid dissolution of evidence for a center of origin as well as the potential birth of a new center of origin. Given the diversity of ecological regions within the three major geological provinces of the Colorado Plateau, Great Basin, and Mojave desert, the complexity of a widely distributed complex – with taxa represented in all three regions – is to be expected even at the infraspecific level. The model of a center of origin, rather than being faulty and misleading as some have suggested, provided the foundational hypothesis that led to the inferences demonstrating corroborative centers of allelic diversity and taxonomic diversity, as well as an investigation of apparent hybridization. In that respect, it was a productive endeavor that will lead to further investigations.

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TABLE 4.1. Nei's gene diversity index (*Hj*) for sampled *E. corymbosum* populations. Populations are listed in order of increasing diversity.

Variety	Diversity Level	Pop #	n	# loc	#loc_P	PLP	*Hj*
nilesii	1	N06	6	103	29	28.2	0.05531
nilesii	2	N02	9	103	33	32	0.05691
nilesii	3	N05	8	103	12	11.7	0.05836
nilesii	4	N04	6	103	27	26.2	0.06076
nilesii	5	N07	8	103	33	32	0.06989
orbiculatum	6	U16	6	103	24	23.3	0.07237
nilesii	7	N08	4	103	27	26.2	0.07619
nilesii	8	N09	6	103	30	29.1	0.07769
nilesii	9	N03	8	103	36	35	0.08088
nilesii	10	N01	8	103	34	33	0.08227
orbiculatum	11	U11	6	103	27	26.2	0.08772
nilesii	12	N10	8	103	33	32	0.08809
glutinosum	13	A01	6	103	31	30.1	0.09459
velutinum	14	A02	6	103	34	33	0.097
glutinosum	15	U14	10	103	36	35	0.09815
corymbosum	16	U12	10	103	34	33	0.10058
velutinum	17	U28	10	103	42	40.8	0.10225
corymbosum	18	U13	10	103	33	32	0.10315
aureum	19	U34	9	103	40	38.8	0.1033
corymbosum	20	U22	10	103	40	38.8	0.10411
orbiculatum	21	U17	7	103	31	30.1	0.1067
aureum	22	U35	10	103	40	38.8	0.10976
corymbosum	23	U23	10	103	39	37.9	0.11128
aureum	24	U36	7	103	39	37.9	0.11246
corymbosum	25	U09	5	103	27	26.2	0.11418
orbiculatum	26	U30	7	103	35	34	0.1153
velutinum	27	U29	8	103	38	36.9	0.12214
aureum	28	N11	10	103	41	39.8	0.12234
glutinosum	29	U08	3	103	24	23.3	0.12288
orbiculatum	30	U31	7	103	35	34	0.12554
aureum	31	U01	8	103	37	35.9	0.13161
aureum	32	U02	7	103	39	37.9	0.14531

TABLE 4.2. Comparisons of frequencies of shared alleles between *E. thompsoniae*, *E. corymbosum* var. *aureum*, and *E. corymbosum* var. *nilesii*.

Band	Freq In var. *nilesii*	Freq In var. *aureum*	Freq In *E. thompsoniae*	Freq In all others
270	0.044	0.235	0.847	0.010
179	0.070	0.188	0.516	0.005
226	0.057	0.688	0.111	0.011
79	0.097	0.459	0.260	0.122
232	1.000	0.779	0.658	0.099
102	0.808	0.729	0.875	0.003
138	1.000	0.688	0.938	0.231
274	0.044	0.050	0.169	0.003
276	0.324	0.251	0.111	0.017
281	0.615	0.117	0.032	0.004
328	0.084	0.050	0.016	0.000
134	0.615	0.416	0.058	0.065
156	0.843	0.531	0.095	0.032
166	0.184	0.145	0.016	0.007
176	0.752	0.174	0.053	0.031
233	0.728	0.356	0.032	0.060
264	0.064	0.130	0.008	0.004
82	0.154	0.050	0.317	0.030

FIG. 4.1. Sampled populations of *Eriogonum corymbosum* varieties: Eca = *aureum*, Ecc = *corymbosum*, Ecg = *glutinosum*, Ecn = *nilesii*, Ecv = *velutinum*, Eco = *orbiculatum*.

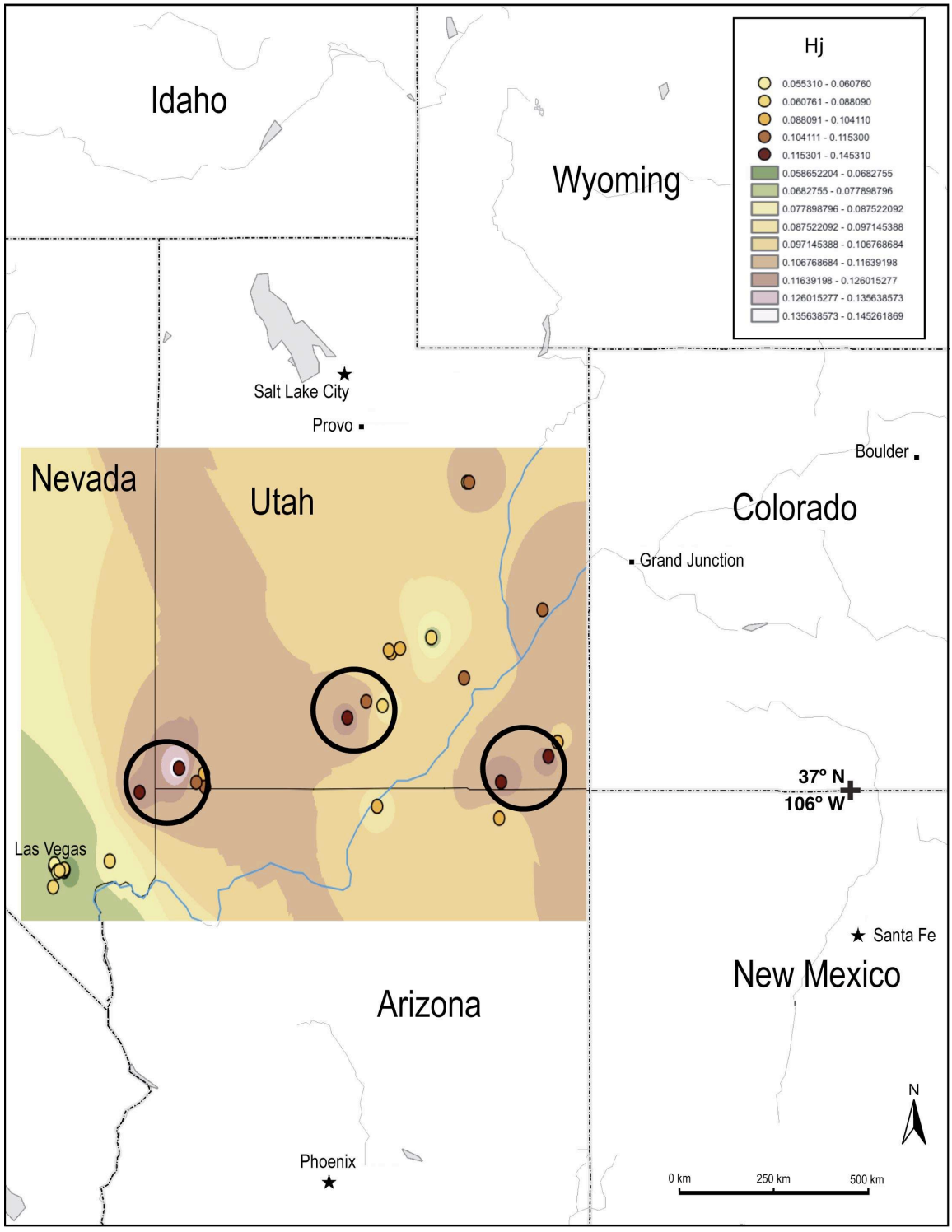

FIG. 4.2. Isocline map predicting within-population genetic diversity (*Hj*) across the landscape based on diversity indices and GPS locations of *E. corymbosum* taxa, with three centers of diversity circled.

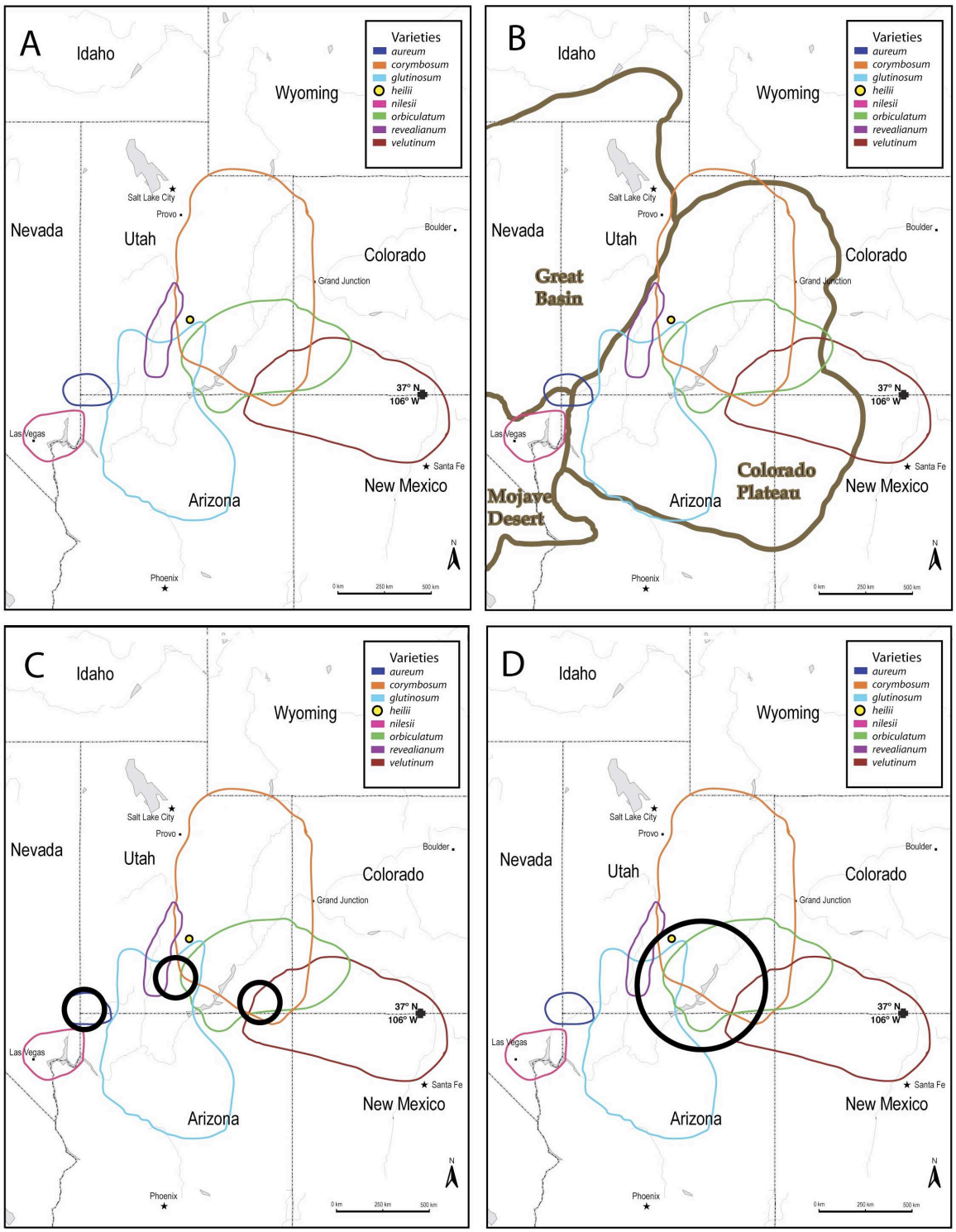

FIG. 4.3. Map A shows the ranges of each *E. corymbosum* variety; the next 3 maps show the relationship between those ranges to three major physiographic regions (map B), the three regions of within-population diversity from Fig. 4.2 (map C), and the putative center of origin for the species (map D).

CHAPTER 5

SUMMARY

When I began this project, I set out to determine whether or not genetic evidence would support the separate varietal designation *nilesii* for those *Eriogonum corymbosum* populations found in Nevada's Las Vegas Valley. I found that the evidence, based on the markers we used, did support that nomenclatural change. But during the process of that investigation, the project necessarily expanded to an exploration of the biogeographical distribution and putative history of this wide-ranging buckwheat species, along with an evaluation of the species concept itself.

The taxon of interest in that initial study, *E. corymbosum* var. *nilesii*, had a confusing nomenclatural history (Reveal 2002, 2005) in which it was lumped with either of two yellow-flowered buckwheat varieties in the *E. corymbosum* complex – one of which (var. *aureum*) has also had a varied nomenclatural past (Jones 1903; Reveal 1967, 2005; Welsh et al. 2003). This history attests to the complexities of infraspecific taxa and the challenges inherent in their determinations. With these challenges in mind, I felt an inquiry into the nature of taxonomic designations would be valuable. That inquiry led me to discover that the species concept itself has been, and remains to this day, a subject of heated debate. Without a clear consensus on this foundational concept, research conclusions will be burdened by an unfortunate level of uncertainty that can complicate management decisions and spark unnecessary political debate.

Fortunately, I found that these debates about species concepts were, like taxonomy itself, hierarchical in nature, and reconcilable. Such debates form part of the

healthy, though often heated, process for which science is known. There are many competing species concepts, but nearly all of those are methodological rather than ontological. Each provides a means to identify a species, and although they differ in their approaches, most of them compliment rather than contradict one another. Depending on the organism or the tools available, one concept may be better than another in identifying and delineating a species. But no single one is best in all situations, and they all can be subsumed under an overall species concept – one that has been understood for decades. Yet the tenor of the debates suggest that the very nature and reality of species is in question, which simply is not the case.

With so many contemporary concepts competing for supremacy, combined with a history of debates about the existence and nature of species that reaches back to the ancient Greeks (Mayer 1950; Hull 1965; Jones 1969; Loomis 1969; Mayr 1982), many consider this long-lived and perplexingly multifaceted problem to be insoluble – one that has always existed and therefore always will. After finding that the nature of the debates hinges mainly on a hierarchical misunderstanding (Ghiselin 2002), bolstered by a plethora of historical challenges that have, by and large, been resolved, I recognized that this problem was largely mythical. It has taken on a life of its own, beyond the arguments. My purpose was to expose this problem as one that has been blown out of proportion. Species are real entities that can be identified (Ghiselin 1974; Hull 1976; Mayden 1999, 2002; Wiley and Mayden 2000), and part of the evolutionary process is the radiation of species that emerge from infraspecific taxa. Although not separate entities like species, infraspecific taxa have the potential to become so, and are critical components of biodiversity, enabling a species like *E. corymbosum* to expand broadly

across the landscape (Moritz 2002; Kulathinal and Singh 2008). With the confidence of that viewpoint in mind, I returned to the *E. corymbosum* complex to examine it from a biogeographical perspective.

Exploring the *E. corymbosum* complex using a center-of-origin model led to a number of findings worth further investigation. The results suggest that the center of origin for the species was in the central Colorado Plateau. Based on AFLP markers, two varieties on the periphery of the species' range had very different attributes. The populations of variety *nilesii* were the least genetically diverse of all *E. corymbosum* varieties, while some populations of the variety *aureum* were the most genetically diverse. Both varieties appear to be disjunct and relatively rare, and they may be on very different evolutionary tracks. Variety *aureum* apparently has a history of hybridizing with the buckwheat species *E. thompsoniae*. The process of interspecific hybridization combined with selection can lead to potentially dramatic divergence and speciation (e.g. Arnold 1992; Rieseberg et al. 1993; Gross and Rieseberg 2005). Variety *nilesii*, on the other hand, appears to be a peripheral isolate confined to the Mojave Desert. Its apparent disjunction and the harsh environmental conditions also set the stage for divergence and speciation.

Varieties *nilesii* and *aureum* are two of the most narrowly distributed taxa within the *E. corymbosum* complex (Reveal 2005; and see Chapter 3). Given their apparent allopatric distribution, they have the opportunity to separate from the complex as independent lineages. Both appear to be important centers of evolutionary divergence and are dominant shrubs in their respective habitats. Given the relatively narrow distribution of these two taxa, their importance on the landscape, potential for speciation,

and apparent rarity, management plans for their preservation should be established. Rapid human development in both the St. George region in southern Utah (where variety *aureum* is found) and Nevada's Las Vegas Valley (where variety *nilesii* is found) is not only covering habitat with roads and structures, but also increasing the level of off-road recreational activities that damage habitat (Frates et al. 2005; Deacon et al. 2007).

The genetic study of *E. corymbosum* provided confirmatory evidence for the divergence of variety *nilesii*, so that management decisions can be pursued with that in mind. The study suggested future research directions, and also ushered me into an examination of species concepts and taxonomic theory. Bringing some clarity to the species concept and putting that debate largely to rest would eliminate a great deal of unnecessary vexation, as well as wasted time and expense, in debating the existence and value of taxa – time and effort that could otherwise be better and productively applied to the very real problems of ecosystem management. It would also remove a tool (or weapon) used by disingenuous parties seeking to disrupt serious efforts to preserve biodiversity and ecosystem health. The biogeographical examination broadens the view of this buckwheat species on the landscape and points to future work as well. The *E. corymbosum* complex offers an ideal subject for further research into the pattern and process of speciation and biogeography.

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APPENDIX

TABLE A.1. *Eriogonum* collection sites listed in alphabetical order by: taxon; coded site name; general location; latitude and longitude.

E. brevicaule; U07; City Canyon, Salt Lake Co, UT; N40 48 29.9 W111 52 2.3. *E. corymbosum aureum*; U01; Shivwits, Washington Co, UT; N37 10 53.5 W113 46 09.2. *E. corymbosum aureum*; U34; Washington, Washington Co, UT; N37 7 51.9 W113 29 9.4. *E. corymbosum aureum*; U35; Beehive Dome, Washington Co, UT; N37 0 35.4 W113 28 7. *E. corymbosum aureum*; U36; 1 km E of Bloomington, Washington Co, UT; N37 3 4.2 W113 34 25.4. *E. corymbosum corymbosum*; U09; Escalante, Garfield Co, UT; N37 47 6.9 W111 37 52.5. *E. corymbosum corymbosum*; U12; Grover, Wayne Co, UT; N38 13 36.9 W111 20 48.2. *E. corymbosum corymbosum*; U13; 3.5 km NW of Grover, Wayne Co, UT; N38 15 1.7 W111 22 26.5. *E. corymbosum corymbosum*; U22; Middle 9-Mile Canyon, Carbon Co, UT; N39 46 32.9 W110 28 47.1. *E. corymbosum corymbosum*; U23; Middle 9-Mile Canyon, Carbon Co, UT; N39 46 30.2 W110 27 21.1. *E. corymbosum glutinosum*; U08; 16 km NE of Henrieville, Garfield Co, UT; N37 38 20.4 W111 50 37.8. *E. corymbosum glutinosum*; U14; 2 km S of Fruita, Wayne Co, UT; N38 15 59.4 W111 14 41.3. *E. corymbosum glutinosum*; A01; 9 km S of Page, Coconino County, AZ.; N36 50 15.5 W111 30 31.1. *E. corymbosum nilesii*; N01; N Las Vegas, Clark Co, NV; N36 17 29.4 W 115 11 47.1. *E. corymbosum nilesii*; N02; N Las Vegas, Clark Co, NV; N36 18 52.1 W115 11 35.8. *E. corymbosum nilesii*; N03; NW Las Vegas, Clark Co, NV; N36 14 54.5 W115 09 20.6. *E. corymbosum nilesii*; N04; NW Las Vegas, Clark Co, NV; N36 14 16.9 W115 09 34.7. *E. corymbosum nilesii*; N05; NW Las Vegas, Clark Co, NV; N36 14 35.4 W115 04 45.3. *E. corymbosum nilesii*; N06; NW Las Vegas, Clark Co, NV; N36 15 30.2 W115 04 22.7. *E. corymbosum nilesii*; N07; S Las Vegas, Clark Co, NV; N36 06 14.9 W115 12 29.7. *E. corymbosum nilesii*; N08; NW Las Vegas, Clark Co, NV; N36 15 58.2 W115 04 43.5. *E. corymbosum nilesii*; N09; NW Las Vegas, Clark Co, NV; N36 14 59.6 W115 08 07.0. *E. corymbosum nilesii*; N10; White Basin, Clark County, NV; N36 20 26.7 W114 33 37.3. *E. corymbosum N11*; N11; 22 km nw of Mesquite, AZ in Lincoln Co, NV; N36 57 42.1 W114 13 5.8. *E. corymbosum orbiculatum*; U11; 14 km E of Escalante, Garfield Co, UT; N37 44 58.6 W111 26 38.0. *E. corymbosum orbiculatum*; U16; 15 km W of Hanksville, Wayne Co, UT; N38 21 56.9 W110 53 11.9. *E. corymbosum orbiculatum*; U17; Three Forks, Wayne Co, UT; N38 00 2.5 W110 30 46.4. *E. corymbosum orbiculatum*; U30; Arches, Grand Co, UT; N38 37 3.8 W109 37 5.4. *E. corymbosum orbiculatum*; U31; 22 km S of Mexican Hat, San Juan Co, UT; N37 3 21.5 W110 5 27.3. *E. corymbosum velutinum*; U28; 17 km NE of Bluff, San Juan Co, UT; N37 25 5.8 W109 26 47.1. *E. corymbosum velutinum*; U29; Bluff, San Juan Co, UT; N37 17 21.8 W109 32 53.6. *E. corymbosum velutinum*; A02; 13 km E of Kayenta, Navajo Co, AZ; N36 43 48.7 W110 6 42.0. *E. effusum*; C01; 12 km NW of Salida, Chaffee Co, Co; N38 37 12.5 W106 4 42.1. *E. effusum*; C02; 13 km NW of Salida, Chaffee Co, Co; N38 37 59.4 W106 4 45.7. *E. hylophilum*; U20; Upper 9-Mile Canyon, Duchesne Co, UT; N39 52 57.9 W110 13 51.1. *E. hylophilum*; U21; Upper 9-Mile Canyon, Duchesne Co, UT; N39 52 57.2 W110 14 6. *E. lancifolium*; U24; 8 km E of Wellington, Carbon Co, UT; N39 32 48.3 W110 38 34.6. *E. leptocladon*; U25; 20 km SW of Green River, Emery Co, UT; N38 54 30.3 W110 22 10.0. *E. leptocladon leptocladon*; U15; 3 km S of Hanksville, Wayne Co, UT; N38 20 40.1 W110 42 23.6. *E.*

loganum; U06; Logan, Cache Co, UT; N41 44 25.2 W111 48 25.5. *E. microthecum*; NM1; 20 km W of Shiprock, San Juan Co, NM; N36 49 4.7 W108 54 44.2. *E. microthecum simpsonii*; U18; 6 km N of Kanab, Kane Co, UT; N37 6 16.0 W112 32 55.6. *E. nummulare*; U10; 17 km N of Dugway Proving Ground, Toole Co, UT; N40 20 12.7 W112 36 47.0. *E. racemosum*; U05; N Salt Lake City, Salt Lake Co, UT; N40 47 28.5 W111 51 42.7. *E. smithii*; U26; Little Flat Top, Emery Co, UT; N38 32 15 W110 29 38.5. *E. smithii*; U27; N Texas Hill, Emery Co, UT; N38 30 2.6 W110 24 47.8. *E. thompsoniae*; U32; 4 km W of Bloomington Hills, Washington Co, UT.; N37 03 16.2 W113 39 54.7. *E. thompsoniae*; U33; 4 km SE of Hurricane, Washington Co, UT; N37 08 53.2 W113 15 20.6. *E. thompsoniae*; U03; La Verkin, Washington Co, UT; N37 13 8.6 W113 15 0. *E. thompsoniae*; U04; Rockville, Washington Co, UT; N37 9 42.4 W113 1 56.6. *E. thompsoniae matthewsiae*; U19; SW Zion Ntl Park, Washington Co, UT; N37 11 47.4 W112 59 33.7.

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